PhytoKeys

PhytoKeys 239: 73–105 (2024)
DOI: 10.3897/phytokeys.239.112563

Research Article

An updated infrageneric classification of the pantropical species-rich genus *Garcinia* L. (Clusiaceae) and some insights into the systematics of New Caledonian species, based on molecular and morphological evidence

Myriam Gaudeul[1*], Patrick Sweeney[2*], Jérôme Munzinger[3]

1 *Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum National d'Histoire Naturelle-CNRS-SU-EPHE-UA, 57 rue Cuvier, CP 39, 75231 Paris, Cedex 05, France*
2 *Yale Peabody Museum, Yale University, 170 Whitney Avenue, New Haven, CT 06511, USA*
3 *AMAP, University of Montpellier, IRD, INRAE, CIRAD, CNRS, Montpellier, France*
Corresponding authors: Myriam Gaudeul (gaudeul@mnhn.fr); Patrick Sweeney (patrick.sweeney@yale.edu)

Abstract

Garcinia L. is a pantropically distributed genus comprised of at least 250 species of shrubs and trees and has centers of diversity located in Africa/Madagascar, Australasia, and Southeast Asia. The genus is notable due to its extreme diversity of floral form, common presence in lowland tropical rainforests worldwide, and potential pharmacological value. Across its entire geographic range, *Garcinia* lacks a recent taxonomic revision, with the last genus-level taxonomic treatment of *Garcinia* conducted over 40 years ago. In order to provide an evolutionary-based framework for a revised infrageneric classification of the genus and to investigate in more detail the systematics of New Caledonian species, we conducted molecular phylogenetic analyses using DNA sequence data for the nuclear ITS region on all samples, and for three chloroplast intergenic spacers (*psbM-trnD*, *trnQ-rps16* and *rps16-trnK*) on a subset of our overall sampling. Our phylogenetic analyses are the most comprehensive to date for the genus, containing 111 biogeographically and morphologically diverse *Garcinia* species. The analyses support a broad circumscription of *Garcinia*, including several previously segregated genera (e.g. *Allanblackia*, *Clusianthemum*, *Ochrocarpos* p.p., *Pentaphalangium*, *Rheedia*, and *Tripetalum*). We recovered nine major clades falling within two major lineages, and we delimit 11 sections. We discuss each of the clades, assign them sectional names, discuss their distinguishing morphological features, compare our taxonomic treatment with the most recent sectional treatment, list representative species, note geographic distribution, and highlight some questions that deserve future investigations. We propose nine new nomenclatural combinations, four new names, and three new lectotypes. In New Caledonia (NC), a total of ten, all endemic, species are recognized and were included in our phylogenetic analyses, with several replicates per species (with the exception of *G. virgata* and *G. urceolata*, represented by a single accession each). New Caledonian species were retrieved within three separate clades, respectively including 1) *G. balansae*; 2) *G. comptonii*, *G. neglecta*, *G. urceolata*, *G. virgata*; and 3) *G. amplexicaulis*, *G. densiflora*, *G. pedicellata*, *G. puat*, *G. vieillardii*. Within NC, the phylogenies did not support the distinction between a putative undescribed species and *G. balansae*. However, it confirmed the distinction between NC species and both *G. vitiensis* (found in Fiji and Vanuatu) and *G. adinantha* (found in Fiji), suggesting that all NC species should be considered as endemics.

OPEN ACCESS

Academic editor: Manuel Luján
Received: 5 October 2023
Accepted: 8 February 2024
Published: 15 March 2024

Citation: Gaudeul M, Sweeney P, Munzinger J (2024) An updated infrageneric classification of the pantropical species-rich genus *Garcinia* L. (Clusiaceae) and some insights into the systematics of New Caledonian species, based on molecular and morphological evidence. PhytoKeys 239: 73–105. https://doi.org/10.3897/phytokeys.239.112563

Copyright: © Myriam Gaudeul et al.
This is an open access article distributed under terms of the CC0 Public Domain Dedication.

* These two authors contributed equally.

Key words: Androecium, floral diversity, *Garcinia*, infrageneric classification, molecular phylogeny, morphological characters, New Caledonia, taxonomy

Introduction

Species rich, morphologically diverse genera can benefit from the delimitation of natural infrageneric groups, which can help to facilitate future monographic work, ecological and evolutionary research, and conservation efforts (van Welzen et al. 2009; Moonlight et al. 2018; Atkins et al. 2021). *Garcinia* L. is a large genus with centers of species diversity located in Africa/Madagascar, Australasia, and Southeast Asia. The genus exhibits extreme diversity of floral morphology, particularly in the androecium and is of high ecological significance with many species forming an important component of the lower strata of lowland tropical forests worldwide. *Garcinia* is also of high economic significance since many species have edible fruits (especially *G. mangostana*) and/or possible medicinal properties (e.g., Pedraza-Chaverri et al. 2008; Espirito Santo et al. 2020).

Recent phylogenetic and biogeographic studies (e.g. Sweeney 2008; Ruhfel et al. 2011; Ruhfel et al. 2016) support a broad circumscription of *Garcinia* that justifies the inclusion of several previously segregated genera (e.g. *Ochrocarpos* Thouars p.p., *Pentaphalangium* Warb., *Rheedia* L., and *Tripetalum* K. Schum.). When broadly circumscribed, the genus contains at least 250 species (Stevens 2007) and maybe as many as ca. 400 (POWO 2023). While some of these molecular studies (Sweeney 2008) revealed major clades with suites of shared morphological characters, no recent genus-wide infrageneric classification of the genus has been attempted.

Infrageneric taxonomy and classification of *Garcinia*

The taxonomy and systematics of *Garcinia* is made challenging due to several factors including the large number of species, dioecy, extreme floral diversity in the paleotropics (particularly in the androecium), poor preservation state of some features (e.g. fruits and flowers) on herbarium specimens, and numerous geographic sites harboring sympatric species. Several valuable efforts have been made to bring taxonomic order to the genus, at various geographic and taxonomic scales.

Previous taxonomic treatments over the past 200 years have resulted in more than 50 infrageneric taxa (Jones 1980). In the most recent worldwide taxonomic treatment of the genus and the benchmark against which more recent genus-level taxonomic work has been evaluated, Jones (1980) recognized 14 sections (Table 1). This treatment relied heavily on staminate flower and pollen morphology to classify upwards of 345 named species. Prior to Jones (1980), the most recent taxonomic treatment of the genus was that of Engler (1894, 1925), which recognized 34 sections. That work was an elaboration of Pierre (1883), who produced the first monograph of *Garcinia* (excluding *Ochrocarpos* and *Rheedia*) and used largely flower and inflorescence characters to classify 149 species into 37 sections that were organized into six groups. The only other monograph of the genus is that of Vesque (1893) who used floral morphology and leaf anatomy to classify 180 species (excluding *Rheedia*) into three

subgenera and nine sections. The first major, global treatment of *Garcinia* (but narrowly circumscribed and not including the segregate genera *Discostigma*, *Ochrocarpos*, *Rheedia*, and *Xanthochymus*) was that of Planchon and Triana (1860), who used mostly floral characters to group 32 species into six sections.

In addition to the above-mentioned works that are global in scope, there have been several noteworthy publications that have dealt with the genus at narrower geographic or taxonomic scales. These studies include work on species in Africa (Sosef and Dauby 2012), Australia (Cooper 2013), Brazil (Mouzinho et al. 2022), China (Li et al. 2007), Colombia (Medellín Zabala 2015), India (Maheshwari 1964; Singh 1993; Mohanan et al. 2023), and Madagascar (Sweeney and Rogers 2008; Rogers et al. 2011).

Two notable recently published works dealing with the infrageneric classification of *Garcinia* are that of Nazre et al. (2018), who provided a monograph for section *Garcinia* and the molecular phylogenetic study of Sweeney (2008) who evaluated Jones' (1980) classification in relation to phylogeny and morphology. Some major findings of Sweeney (2008) were that some segregated genera should be included within *Garcinia*, and while partly congruent with phylogeny, the infrageneric sectional classification of Jones (1980) needs revision.

Taxonomy of New Caledonian *Garcinia* species

In contrast to other regions cited above, and in spite of the observed diversity within *Garcinia* in New Caledonia (NC), an archipelago that is well-known for its high overall levels of botanical diversity and endemism (Morat et al. 2012; Munzinger et al. 2023), the genus has not been recently and thoroughly studied in this territory. Only one species (*G. amplexicaulis*) was included in the phylogeny of Sweeney (2008). One species was recently described (Munzinger et al. 2021), leading to a total of ten –all presumed endemic– species, but the circumscription of some species is unclear and some questions remain about the conspecificity or, at least, the close evolutionary relationships between some non-NC and NC species that appear morphologically similar.

A taxon resembling *G. balansae* grows on the ultramafic massifs in the northwest of NC, but it displays linear, erect leaves and a very cracked greyish bark compared to the brownish and smoother bark of *G. balansae* (Fig. 1). This putative new taxon (*G.* sp. "JT814") is restricted to three massifs (Boulinda, Koniambo and Tiébaghi) and should be considered as Endangered (Lowry and Munzinger 2015), but its taxonomic rank remains unresolved. In addition, the Fijian *G. vitiensis* (A. Gray) Seem. is cited in NC by Sebert and Pancher (1874), but the material of this species is then assigned by Pierre to his endemic species: *G. balansae* Pierre. Strangely, Pierre (1883: XXXVI) states "that he has never seen material of *G. vitiensis*, appearing close to *G. balansae*" (our translation). The conspecificity or non conspecificity between the two taxa remains to be tested. The presence of *G. sessilis* Seem. in NC is also mentioned at the end of the 19th and in the early 20th century (Sebert and Pancher 1874; Hemsley 1895), while subsequent authors considered this species as a Fijian endemic (Smith and Darwin 1974; Smith 1981) without discussion about its potential occurrence in NC. *Garcinia sessilis* was later split into two species, with the description of *G. adinantha* A.C.Sm. & S.P.Darwin (Smith and Darwin 1974), but the evolutionary relationship between the New Caledonian and these two Fijian species remains unknown.

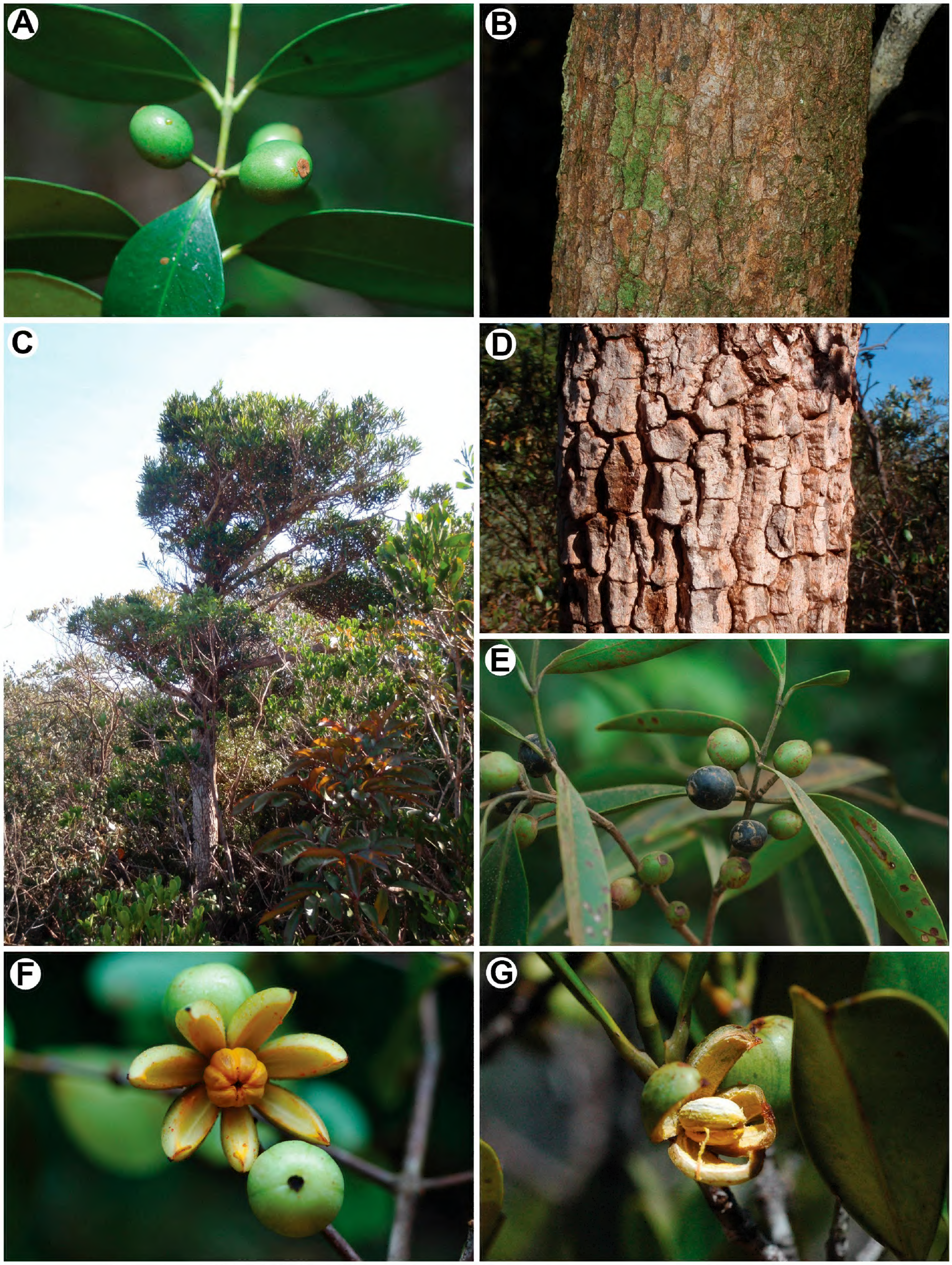


Figure 1. Some *Garcinia* New Caledonian species (except E from Fiji) and morphological features **A** *G. balansae* (Munzinger 4916), fruiting branch **B** *G. balansae* (Munzinger 4916), bark **C** *G.* sp. "JT814" (Munzinger 7282), habit **D** *G.* sp. "JT814" (Munzinger 7282), bark **E** *G. vitiensis* (Munzinger 7377), fruiting branch **F** *G. neglecta* (Munzinger 2690), fruit **G** *G. comptonii* (sin voucher), fruit.

Based on an enlarged taxonomic sampling compared to Sweeney (2008), and an important sampling effort in the Pacific Ocean region and NC in particular (including several samples per morphologically delimited species), our goal is to provide an updated molecular phylogeny of the genus in order: 1) to offer a way forward on a revised infrageneric classification of *Garcinia* considering both morphological and molecular evidence; and 2) to provide insight into the systematics of NC species.

Materials and methods

Taxonomic sampling

This study was based on both published and newly generated sequences, leading to a total of 160 samples representing 121 species (including ten outgroups) and two putative new species (*G.* sp. "JT814" from NC and *G.* sp. Munzinger 7380 from Fiji; Suppl. material 1). Published sequences included sequences from Sweeney (2008; 57 sequences), in addition to 25 sequences downloaded from Genbank and three sequences taken from Nazre (2006). New ITS sequences were generated from both herbarium and silica-dried leaf material collected in the field. They included a total of 72 samples representing 39 species and two unidentified taxa, among which were 32 samples representing 10 species and one unidentified taxon from NC (Suppl. material 1). The sampling comprised representatives of all major *Garcinia* clades based on Sweeney (2008) and *Allanblackia*, and covered both the morphological diversity and biogeographic range of *Garcinia*. The outgroup included seven genera: *Lorostemon* Ducke, *Montrouziera* Pancher ex Planch. & Triana, *Moronobea* Aubl., *Pentadesma* Sabine and *Symphonia* L.f. from the Symphonieae tribe, and *Arawakia* L.Marinho and *Clusia* L. from the Clusieae tribe. A subset of this sampling was used to generate a fully original chloroplast DNA dataset: it comprised 67 samples representing 45 species (among which was one outgroup) and two putative new species (see above), covering all *Garcinia* clades based on Sweeney (2008) and including nine out of the ten NC *Garcinia* species.

DNA sequencing

DNA extraction was performed with the DNeasy Plant Mini Kit (QIAGEN, Courtaboeuf, France), following the manufacturer's protocol except for a slight modification: we added 30 µL CTAB and 30 µL proteinase K for the initial digestion, which lasted 24h at 42 °C. The nuclear ribosomal ITS region included the two transcribed intergenic spacers ITS1 and ITS2, separated by the 5.8S gene. It was sequenced using either the primers ITS4 and ITS5 (White et al. 1990) or the newly designed primers ITS4Garci (5'-CCTGACCTGGGGTCGC-3') and ITS5Garci (5'-AACCTGCGGAAGGATCATTG-3') that were more specific to *Garcinia* or at least to angiosperms, minimizing the risk of false positive due to fungi amplification when the amount of plant DNA was too low as a PCR template. Three chloroplast intergenic spacers were also sequenced: *psbM-trnD*, *trnQ-rps16* and *rps16-trnK*. PCR primers were psbMF and trnD^{GUC}R for *psbM-trnD* (Shaw et al. 2005), trnQ^{UUG} and rps16x1 for *trnQ-rps16* (Shaw et al. 2007) and rpS16x2F2 and trnK^{UUU}x1 for *rps16-trnK* (Shaw et al. 2007). All PCRs

were performed in 25 µL including 1X Taq Buffer, 2.5 mM $MgCl_2$, 1M betaine, 0.25 mM of each dNTP, 0.4 µM of each primer, 0.6U Taq polymerase and 1 µL template DNA. PCR conditions were: 94 °C for 5 min, followed by 40 cycles of: 94 °C 30 sec, Tm 45 sec, 72 °C 1 min, and a final extension step of 10 min at 72 °C. Tm was 48 °C for ITS and *psbM*-trnD, 44 °C for *trnQ-rps16*, and 46 °C for *rps16-trnK*. PCR products were sequenced in both directions by Eurofins (Evry, France), using the same primers as for the PCRs. Sequences were automatically aligned in MUSCLE v3.6 (Edgar 2004) before the alignments were manually revised in BioEdit v.7.2.5 (Hall 1999). Indels were coded following the simple coding method of Simmons and Ochoterena (2000) implemented in SeqState (Müller 2005). Vouchers details are listed in Suppl. material 1.

Phylogenetic reconstructions

First, individual analyses were carried out on each DNA region. Bayesian inferences (BI) were performed using MrBayes v.3.1.2 (Ronquist et al. 2011). For each region, the best-fitting model of nucleotide substitution was identified under the Akaike information criterion in MrModelTest v.2.3 (Nylander 2004): GTR + I + Γ for the ITS region and psbM-trnD intergenic spacer, and GTR + Γ for the trnQ-rps16 and rps16-trnK intergenic spacers (using distinct models for ITS1, ITS2 and 5.8S did not make any difference in the resulting tree). For indels, we used the restriction site (binary) model, with the option lset coding = variable. Two independent but parallel analyses were conducted using flat priors, starting from random trees and consisting of four chains each. The analyses were run for 6 million generations, sampling every 1000 generations and with a 25% burn-in. Analysis of output parameters, in Tracer v.1.6 (Rambaut et al. 2014), confirmed the convergence of chains and adequate burn-in length. Post-burn-in trees were pooled and a 50% majority-rule consensus tree was computed with posterior probability (PP) estimates for all nodes. Maximum likelihood (ML) was also used to estimate phylogenetic relationships. The ML analysis was performed in raxmlGUI 1.5.1 (Silvestro and Michalak 2012; Stamatakis 2014), using the same partitions and models of nucleotide evolution as for the BI. We performed 1000 rapid bootstrap (BS) replicates and searched for the best-scoring ML tree. The topologies inferred by BI analyses from each chloroplast marker were visually compared to identify potential incongruence among them (Suppl. materials 2–4). Since no major incongruence was highly supported, the three chloroplast sequences for each sample were then combined to maximise the number of characters analysed in the BI and ML analyses. Also, a BI analysis was performed by merging the nuclear and chloroplast datasets on the reduced sampling (Suppl. material 5).

Results

Large-scale infrageneric phylogeny

The ITS alignment was 773 base pairs (bp) long and 91 indels were coded, whereas the cpDNA alignment was 2484 bp long (795 bp for psbM-trnD, 674 bp for trnQ-rps16 and 1015 bp for rps16-trnK) and 167 indels were coded. Only minor differences were identified among trees using BI and ML, and no conflict

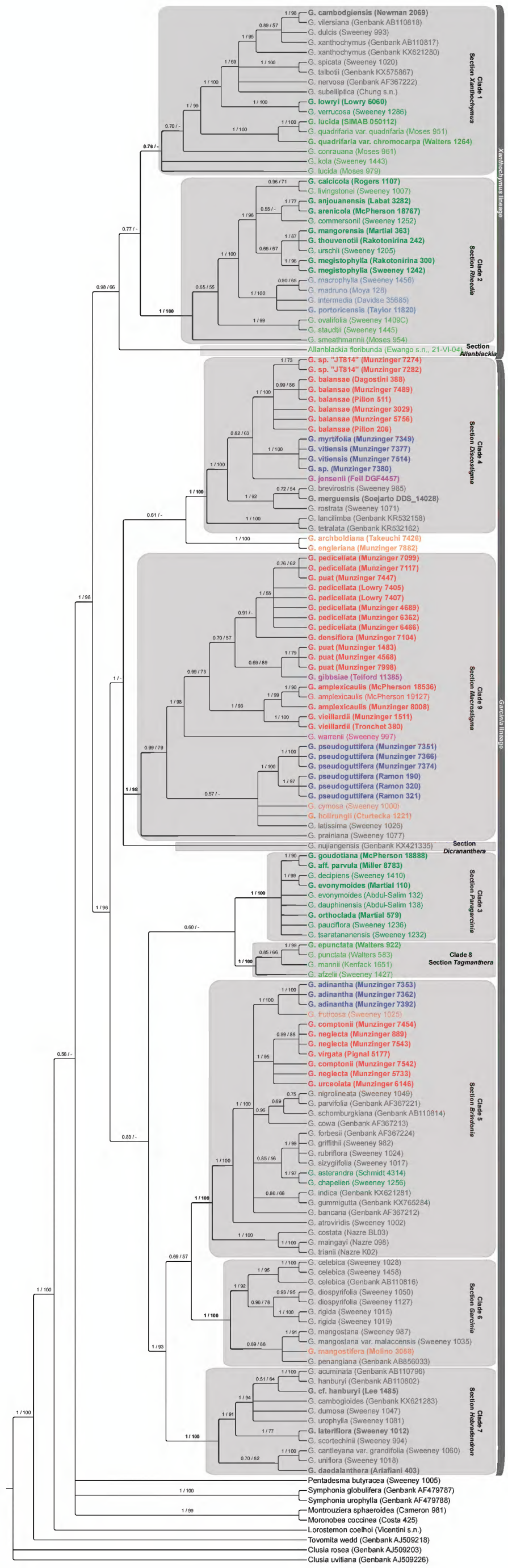
was supported. Because both resolution and support were higher using BI, we chose to present the resulting BI topologies, on which we also indicated the support values obtained from the ML analyses (Figs 2, 3).

Based on ITS, we recovered mostly the same two major lineages and nine clades as Sweeney (2008). The allied genera *Allanblackia*, *Ochrocarpos*, *Pentaphalangium*, *Rheedia*, and *Tripetalum* were again retrieved within *Garcinia*. We retrieved a clade containing clade 1 and clade 2, which corresponds to Lineage A in Sweeney (2008). Its support was PP = 0.77 (vs. 0.99 in Sweeney 2008) and it was not retrieved in ML. Nevertheless, the clade consisting of lineage A of Sweeney (2008) and *Allanblackia floribunda* was more strongly supported (PP = 0.98, BS = 66). Clade 1 was not highly supported in BI (PP = 0.76 vs. 0.98 in Sweeney 2008) and not fully retrieved in ML. This was due to three species: *G. conrauana*, *G. kola* and *G. lucida*. The support of clade 1 excluding these three species reached PP = 1 and BS = 99. Compared to Sweeney (2008), nine new species were assigned to this clade (five downloaded from Genbank, three newly sequenced and *G. conrauana*). Clade 2 was strongly supported (PP = 1, BS = 100). Seven newly sequenced species were assigned to this clade. A clade corresponding to Lineage B of Sweeney (2008) consisted of clades 3 to 9 and three additional species, *G. engleriana*, *G. archboldiana* and *G. nujiangensis*, which were not included in any major clade. The Lineage B clade was highly supported (PP = 1, BS = 96) and all major subclades also received strong support (all PP = 1 and all BS = 100 except for clade 9, BS = 98). They included one (in clade 8) to 15 (in clade 5) additional species each compared to Sweeney (2008). Relationships between clades remained largely unresolved. No grouping was supported except the one including clades 5, 6 and 7 (PP = 1, BS = 93), as was observed by Sweeney (2008).

Based on the combined chloroplast dataset, the same nine clades were retrieved with high support (all PP = 1 and BS from 93 to 100). The only allied genus included in the analysis was *Pentaphalangium*, which was retrieved within *Garcinia* in agreement with the ITS phylogeny. *Garcinia archboldiana* and *G. engleriana* were again sister species, and not included in any major clade. Clades 1 and 2 grouped together (PP = 1, BS = 81), as did clades 3 and 8 (PP = 0.99, BS = 81), which were sister to clade 4 (PP = 1, BS = 95). Clades 5, 6 and 7 grouped together (PP = 1, BS = 78) and this clade grouped with clade 9 and *G. archboldiana* and *G. engleriana* (PP = 1, BS = 99).

Focus on the New Caledonian species

New Caledonian species were retrieved within three distinct clades: *G. balansae* and *G.* sp. "JT814" were recovered in clade 4; *G. comptonii*, *G. neglecta*, *G. urceolata* and *G. virgata* were placed in clade 5, within which they formed a highly supported subclade (PP = 1 and BS = 95 in the more densely sampled ITS phylogeny); and *G. amplexicaulis*, *G. densiflora*, *G. pedicellata*, *G. puat* and *G. vieillardii* were recovered in clade 9, grouped in a subclade that also included the Australian *G. gibbsiae* (PP = 0.99, BS = 73 in the ITS phylogeny). Together with *G. warrenii*, they formed a strongly supported clade (PP = 1, BS = 98). Within clade 4, the two accessions of *G.* sp. "JT814" formed a subclade based on ITS, but were scattered among the *G. balansae* accessions based on cpDNA. Similarly, the NC species grouped within clades 5 and 9 did not appear reciprocally


G. cambodgiensis (Newman 2069)
G. vilersiana (Genbank AB110818)
G. dulcis (Sweeney 993)
G. xanthochymus (Genbank AB110817)
G. xanthochymus (Genbank KX621280)
G. spicata (Sweeney 1020)
G. talbotii (Genbank KX575867)
G. nervosa (Genbank AF367222)
G. subelliptica (Chung s.n.)
G. lowryi (Lowry 6060)
G. verrucosa (Sweeney 1286)
G. lucida (SIMAB 050112)
G. quadrifaria var. quadrifaria (Moses 951)
G. quadrifaria var. chromocarpa (Walters 1264)
G. conrauana (Moses 961)
G. kola (Sweeney 1443)
G. lucida (Moses 979)
Clade 1 Section Xanthochymus
G. calcicola (Rogers 1107)
G. livingstonei (Sweeney 1007)
G. anjouanensis (Labat 3282)
G. arenicola (McPherson 18767)
G. commersonii (Sweeney 1252)
G. mangorensis (Martial 363)
G. thouvenotii (Rakotonirina 242)
G. urschii (Sweeney 1205)
G. megistophylla (Rakotonirina 300)
G. megistophylla (Sweeney 1242)
G. macrophylla (Sweeney 1456)
G. madruno (Moya 128)
G. intermedia (Davidse 35685)
G. portoricensis (Taylor 11820)
G. ovalifolia (Sweeney 1409C)
G. staudtii (Sweeney 1445)
G. smeathmannii (Moses 954)
Clade 2 Section Rheedia
Xanthochymus lineage
Allanblackia floribunda (Ewango s.n., 21-VI-04)
Section Allanblackia
G. sp. "JT814" (Munzinger 7274)
G. sp. "JT814" (Munzinger 7282)
G. balansae (Dagostini 388)
G. balansae (Munzinger 7489)
G. balansae (Pillon 511)
G. balansae (Munzinger 3029)
G. balansae (Munzinger 5756)
G. balansae (Pillon 206)
G. myrtifolia (Munzinger 7349)
G. vitiensis (Munzinger 7377)
G. vitiensis (Munzinger 7514)
G. sp. (Munzinger 7380)
G. jensenii (Fell DGF4457)
G. brevirostris (Sweeney 985)
G. merguensis (Soejarto DDS_14028)
G. rostrata (Sweeney 1071)
G. lancilimba (Genbank KR532158)
G. tetralata (Genbank KR532162)
Clade 4 Section Discostigma
G. archboldiana (Takeuchi 7426)
G. engleriana (Munzinger 7882)
G. pedicellata (Munzinger 7099)
G. pedicellata (Munzinger 7117)
G. puat (Munzinger 7447)
G. pedicellata (Lowry 7405)
G. pedicellata (Lowry 7407)
G. pedicellata (Munzinger 4689)
G. pedicellata (Munzinger 6362)
G. pedicellata (Munzinger 6466)
G. densiflora (Munzinger 7104)
G. puat (Munzinger 1483)
G. puat (Munzinger 4568)
G. puat (Munzinger 7998)
G. gibbsiae (Telford 11385)
G. amplexicaulis (McPherson 18536)
G. amplexicaulis (McPherson 19127)
G. amplexicaulis (Munzinger 8008)
G. vieillardii (Munzinger 1511)
G. vieillardii (Tronchet 380)
G. warrenii (Sweeney 997)
Clade 9 Section Macrostigma
G. pseudoguttifera (Munzinger 7351)
G. pseudoguttifera (Munzinger 7366)
G. pseudoguttifera (Munzinger 7374)
G. pseudoguttifera (Ramon 190)
G. pseudoguttifera (Ramon 320)
G. pseudoguttifera (Ramon 321)
G. cymosa (Sweeney 1000)
G. hollrungii (Cturtecka 1221)
G. latissima (Sweeney 1026)
G. prainiana (Sweeney 1077)
Garcinia lineage
G. nujiangensis (Genbank KX421335)
Section Dicrananthera
G. goudotiana (McPherson 18888)
G. aff. parvula (Miller 8783)
G. decipiens (Sweeney 1410)
G. evonymoides (Martial 110)
G. evonymoides (Abdul-Salim 132)
G. dauphinensis (Abdul-Salim 138)
G. orthoclada (Martial 579)
G. pauciflora (Sweeney 1236)
G. tsaratananensis (Sweeney 1232)
Clade 3 Section Paragarcinia
G. epunctata (Walters 922)
G. punctata (Walters 583)
G. mannii (Kenfack 1651)
G. afzelii (Sweeney 1427)
Clade 8 Section Tagmanthera
G. adinantha (Munzinger 7353)
G. adinantha (Munzinger 7362)
G. adinantha (Munzinger 7392)
G. fruticosa (Sweeney 1025)
G. comptonii (Munzinger 7454)
G. neglecta (Munzinger 889)
G. neglecta (Munzinger 7543)
G. virgata (Pignal 5177)
G. comptonii (Munzinger 7542)
G. neglecta (Munzinger 5733)
G. urceolata (Munzinger 6146)
G. nigrolineata (Sweeney 1049)
G. parvifolia (Genbank AF367221)
G. schomburgkiana (Genbank AB110814)
G. cowa (Genbank AF367213)
G. forbesii (Genbank AF367224)
G. griffithii (Sweeney 982)
G. rubriflora (Sweeney 1024)
G. sizygiifolia (Sweeney 1017)
G. asterandra (Schmidt 4314)
G. chapelieri (Sweeney 1256)
G. indica (Genbank KX621281)
G. gummigutta (Genbank KX765284)
G. bancana (Genbank AF367212)
G. atroviridis (Sweeney 1002)
G. costata (Nazre BL03)
G. maingayi (Nazre 098)
G. trianii (Nazre K02)
Clade 5 Section Brindonia
G. celebica (Sweeney 1028)
G. celebica (Sweeney 1458)
G. celebica (Genbank AB110816)
G. diospyrifolia (Sweeney 1050)
G. diospyrifolia (Sweeney 1127)
G. rigida (Sweeney 1015)
G. rigida (Sweeney 1019)
G. mangostana (Sweeney 987)
G. mangostana var. malaccensis (Sweeney 1035)
G. mangostifera (Molino 3058)
G. penangiana (Genbank AB856033)
Clade 6 Section Garcinia
G. acuminata (Genbank AB110796)
G. hanburyi (Genbank AB110802)
G. cf. hanburyi (Lee 1485)
G. cambogioides (Genbank KX621283)
G. dumosa (Sweeney 1047)
G. urophylla (Sweeney 1081)
G. lateriflora (Sweeney 1012)
G. scortechinii (Sweeney 994)
G. cantleyana var. grandifolia (Sweeney 1060)
G. uniflora (Sweeney 1018)
G. daedalanthera (Ariafiani 403)
Clade 7 Section Hebradendron
Pentadesma butyracea (Sweeney 1005)
Symphonia globulifera (Genbank AF479787)
Symphonia urophylla (Genbank AF479788)
Montrouziera sphaeroidea (Cameron 981)
Moronobea coccinea (Costa 425)
Lorostemon coelhoi (Vicentini s.n.)
Tovomita wedd (Genbank AJ509218)
Clusia rosea (Genbank AJ509203)
Clusia uvitiana (Genbank AJ509226)

monophyletic, neither in the ITS nor in the cpDNA trees (combined analyses, including both ITS and cpDNA data, did not allow a better discrimination). The only exceptions were *G. vieillardii* (two samples from the same locality; PP = 1 and BS = 100 both based on ITS and on cpDNA) and *G. amplexicaulis* (three samples, PP = 1 and BS = 99 based on ITS; only one sample in cpDNA). *Garcinia vieillardii* and *G. amplexicaulis* were also sister species with high support based on ITS (PP = 1 and BS = 93), but not based on cpDNA. Both the ITS and (to a lesser extent) the cpDNA trees show that *G. vitiensis* from Fiji, although belonging to clade 4, was distinct from any of the NC taxa and more related to others Fijian species and to the *G. vitiensis* accession from Vanuatu. In clade 5, *Garcinia adinantha* was also closer to *G. fruticosa* (based on the ITS phylogeny, which was more densely sampled) than to NC species.

Discussion

The previous most comprehensive phylogeny for *Garcinia* (*sensu lato*) included 53 species (Sweeney 2008), and the present study increases this number to 111 and includes a biogeographically and morphologically diverse set of species. This more dense and diverse sampling allows for a robust evaluation of the infrageneric classification of the genus, in relation to the morphology-based sections delineated by Jones (1980). Additionally, the inclusion of 32 samples representing the ten species endemic to New Caledonia provides an opportunity to explore in more depth the evolution and taxonomy of New Caledonian *Garcinia*.

Taxonomy: proposal for an updated infrageneric classification of Garcinia

This study, like others (e.g. Sweeney 2008; Ruhfel et al. 2011; Ruhfel et al. 2016), supports a broad circumscription of *Garcinia* that justifies the inclusion of several previously segregated genera (e.g. *Allanblackia*, *Ochrocarpos* p.p., *Pentaphalangium*, *Rheedia*, and *Tripetalum*). The phylogenetic analyses in this paper and in Sweeney (2008) reveal nine major clades falling within two major lineages and provide a framework for a revised sectional classification of the genus. Seven of the major clades roughly correspond to sections recognized by Jones (1980; Table 1. Of the two remaining major clades, one (clade 2) is a morphologically cohesive group that is comprised chiefly of species that Jones (1980) placed into sections *Rheedia*, *Rheediopsis*, and *Teracentrum*. The other remaining major clade (clade 9) contains primarily species that were placed by Jones (1980)

Figure 2. Molecular phylogeny of *Garcinia* L. based on ITS sequences and Bayesian inference. Posterior probabilities (PP) and bootstrap support values (BS), obtained respectively by the Bayesian inference and Maximum Likelihood (ML) analysis, are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. The lineages/sections discussed in the text are highlighted, and species names appear in colors depending on their native distribution areas: light blue, Central and South America; light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) geographic region was used. Accessions in bold were newly sequenced in this study.

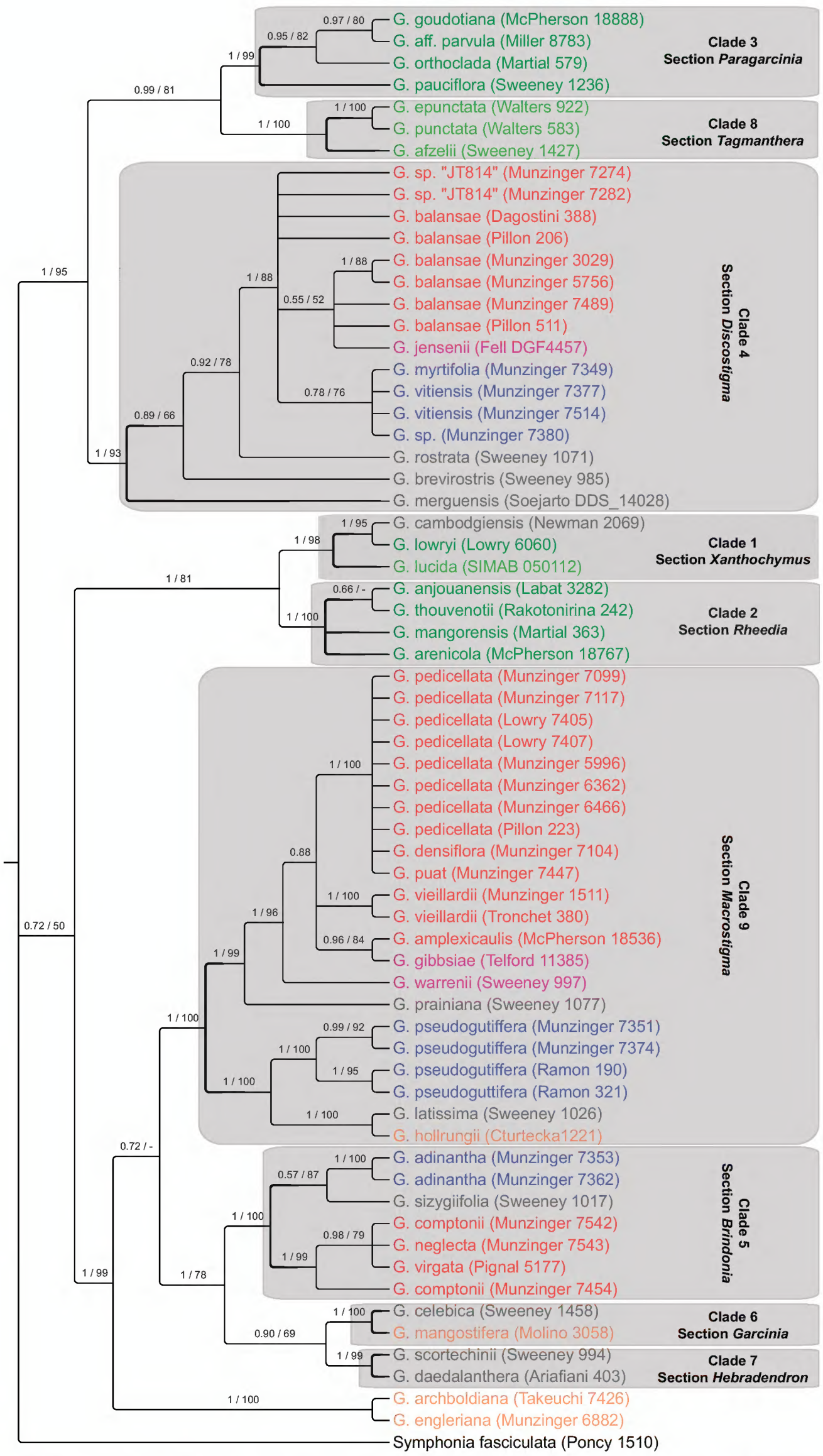


Figure 3. Molecular phylogeny of *Garcinia* L. based on a combined chloroplast DNA dataset and Bayesian inference. Posterior probabilities (PP) and bootstrap support values (BS), obtained respectively by the Bayesian inference and Maximum Likelihood (ML) analysis, are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. The lineages/sections discussed in the text are highlighted, and species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

Table 1. Sections and numbers of species recognized by Jones (1980) and their correspondence to sections and clades recognized in this study. *Allanblackia* was treated as separate from *Garcinia* by Jones (1980).

Section sensu Jones (1980)	No. spp. (sensu Jones 1980)	Clade	Section in this study
Xanthochymus (Roxb.) Pierre	42	1	*Xanthochymus* (Roxb.) Pierre
Tetraphalangium Engl.	2		
Rheediopsis Pierre	20	2	*Rheedia* (L.) S.W.Jones ex P.W.Sweeney
Rheedia (L.) S.W.Jones, *nom. inval.*	21		
Teracentrum Pierre	4		
Paragarcinia (Baillon) Vesque	10	3	*Paragarcinia* (Baillon) Vesque
Discostigma (Haask.) Hook.f. subsection *Discostigma*	53	4	*Discostigma* (Haask.) Hook.f.
Brindonia (Thouars) Choisy	78	5	*Brindonia* (Thouars) Choisy
Garcinia L.	46	6	*Garcinia* L.
Hebradendron (Graham) Planch. & Triana	35	7	*Hebradendron* (Graham) Planch. & Triana
Tagmanthera Pierre	18	8	*Tagmanthera* Pierre
Mungotia Pierre	9	9	*Macrostigma* Pierre
Tripetalum (K. Schum.) S.W.Jones, 1980, *nom. inval.*	1		
Macrostigma Pierre	7		
Discostigma subsection *Dicrananthera* (Pierre) S.W.Jones, *nom. inval.*	2	–	*Dicrananthera* Pierre

into sections *Macrostigma*, *Mungotia*, and *Tripetalum*. Below we discuss each of these clades, providing their distinguishing characteristics and assigning them sectional names, with the aim of laying the foundation for a phylogenetically informed infrageneric classification of *Garcinia*. The distinguishing sectional characters below are taken from the literature and from examination of physical and digitized herbarium specimens (A, BO, CNS, G, GH, K, KEP, KLU, L, MEL, MO, NY, P, PE, SCA, SING, TAN, TEF, US, YU) and plants in the field. We refer readers to Jones (1980) for a detailed account of previous infrageneric classifications of *Garcinia*, along with sectional synonymy. Informed by an examination of specimens, protologues, and Jones' (1980) sectional assignments, we assign accepted species to sections. In cases where protologue descriptions or specimens were insufficient for determining sectional assignment, species were unplaced.

Taxonomic account

Genus *Garcinia* L. Sp. Pl. 1: 443 (1753).

Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Synonyms. *Rheedia* L., Sp. Pl. 2: 1193 (1753). Type. *Rheedia lateriflora* L. [=*Garcinia humilis* (Vahl.) C.D.Adams, Phytologia 20(5): 312 (1970); non *Garcinia lateriflora* Blume, Bijdr. Fl. Ned. Ind. 5: 214 (1825)].

Cambogia L., Gen. Pl., ed. 5: 225 (1754). Type. *Cambogia gummi-gutta* L., Gen. Pl., ed. 5: 225 (1754) [≡*Garcinia gummi-gutta* (L.) N.Robson, Brittonia 20: 103 (1968)].

Coddampuli Adans., Fam. Pl. (Adanson) 2: 445 (1763), *nom. illeg. superfl.* Type: *Cambogia gummi-gutta* L., Gen. Pl., ed. 5: 225 (1754) [≡*Garcinia gummi-gutta* (L.) N.Robson, Brittonia 20: 103 (1968)].

Mangostan Garcin ex Adans., Fam. Pl. (Adanson) 2: 445 (1763), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Biwaldia Scop., Intr. Hist. Nat. 232 (1777), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Stalagmitis Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789). Type. *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789) [≡*Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856)].

Oxycarpus Lour., Fl. Cochinch. 2: 647 (1790). Type. *Oxycarpus cochinchinensis* Lour., Fl. Cochinch. 2: 648 (1790) [≡*Garcinia cochinchinensis* (Lour.) Choisy, Prodr. [A. P. de Candolle] 1: 561 (1824)].

Mangostana Rumph. ex Gaertn., Fruct. Sem. Pl. ii. 105. t. 105. (1791), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Verticillaria Ruiz & Pav., Fl. Peruv. Prodr. 81, t. 15 (1794). Type. *Verticillaria acuminata* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 140 (1798) [=*Garcinia madruno* (Kunth) Hammel, Ann. Missouri Bot. Gard. 76: 928 (1989)].

Ochrocarpos Noronha ex Thouars, Gen. Nov. Madagasc. 15 (1805). Type. *Ochrocarpos madagascarensis* Choisy, Prodr. [A. P. de Candolle] 1: 560 (1824) [non *Ochrocarpos madagascariensis* Planchon & Triana, Ann. Sci. Nat. Bot., sér. 4, 14: 364 (1860)], see Sprague (1934) and Sweeney and Rogers (2008) for discussions about original material of *Ochrocarpos madagascarensis* and the type species of *Ochrocarpos*.

Xanthochymus Roxb., Pl. Coromandel 2(4): 51, t. 196 (1805). Type. *Xanthochymus pictorius* Roxb. [≡*Garcinia xanthochymus* Hook.f. ex T. Anderson Fl. Brit. India [J. D. Hooker] 1(2): 269 (1874)].

Brindonia Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 339 (1806). Type. *Brindonia oxycarpa* Thouars, Hist. Veg. Isles Austr. Afr. ed. 2 t. 27 (1805) [≡*Garcinia oxycarpa* (Thouars) P.W.Sweeney comb. nov.]. See commentary under Section *Brindonia* for details about the status of *B. oxycarpa*.

Chloromyron Pers., Syn. Pl. [Persoon] 2(1): 73 (1806). Type. *Chloromyron verticillatum* Pers., Syn. Pl. [Persoon] 2(1): 73 (1806) [≡*Verticillaria acuminata* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 140 (1798); =*Garcinia madruno* (Kunth) Hammel, Ann. Missouri Bot. Gard. 76: 928 (1989)].

Hebradendron Graham, Companion Bot. Mag. 2: 199 (1837), *nom. illeg. superfl.* (Art. 58.1). Type. *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. Ix. 1787-88 (1789) 173. [≡*Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856); ≡*Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)].

Discostigma Hassk., Flora 25(2, Beibl.): 33 (1842). Type. *Discostigma rostratum* Hassk., Flora 25(2, Beibl.): 33 (1842) [≡*Garcinia rostrata* (Hassk.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 209 (1864)].

Terpnophyllum Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6: 70, t. 2 C (1854). Type. *Terpnophyllum zeylanicum* Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6: 70, t. 2. F. 1 (1854) [≡*Garcinia terpnophylla* Thwaites, Enum. Pl. Zeyl. [Thwaites] 406 (1864)].

Rhinostigma Miq., Fl. Ned. Ind., Eerste Bijv. Pt. 3: 495 (1861). Type. *Rhinostigma parvifolium* Miq., Fl. Ned. Ind., Eerste Bijv. Pt. 3: 495 (1861) (lectotype, designated here) [≡*Garcinia parvifolia* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 208 (1864)].

Clusianthemum Vieill., Bull. Soc. Linn. Normandie 9: 338 (1865). Type. *Clusianthemum pedicellatum* Vieill., Bull. Soc. Linn. Normandie 9: 339 (1865).

Allanblackia Oliv., Gen. Pl. [Benth. & Hook.f.] 1(3): 980 (1867), J. Linn. Soc., Bot. 10: 43 (1867). Type. *Allanblackia floribunda* Oliv., J. Linn. Soc., Bot. 10: 43 (1867).

Pentaphalangium Warb., Bot. Jahrb. Syst. 13(3–4): 382 (1891). Type. *Pentaphalangium crassinerve* Warb., Bot. Jahrb. Syst. 13(3–4): 382 (1891) [≡*Garcinia crassinervis* (Warb.) Kosterm., Ceylon J. Sci., Biol. Sci. 12(1): 68 (1976)].

Tripetalum K.Schum., Fl. Kais. Wilh. Land [K.M. Schumann & M.U. Hollrung] 51 (1889). Type. *Tripetalum cymosum* K.Schum., Fl. Kais. Wilh. Land [K.M. Schumann & M.U. Hollrung] 51 (1889) [≡*Garcinia cymosa* (K.Schum.) I.M.Turner & P.F.Stevens, Gard. Bull. Singapore 51(2): 176 (1999)].

Tsimatimia Jum. & H.Perrier, Ann. Sci. Nat., Bot. sér. 9, 11: 256 (1910). Type. *Tsimatimia pedicellata* Jum. & H.Perrier, Ann. Sci. Nat., Bot. sér. 9, 11: 265 (1910) (lectotype, designated here) [≡*Garcinia tsimatimia* P.W.Sweeney & Z.S.Rogers, Novon 18(4): 535 (2008)].

Septogarcinia Kosterm., Reinwardtia 6: 167 (1962). Type. *Septogarcinia sumbawaensis* Kosterm., Reinwardtia 6: 167 (1962) [≡*Garcinia septogarcinia* I.M. Turner & L.V.S. Jenn; non *Garcinia sumbawensis* Lauterb., Bot. Jahrb. Syst. 58(1): 26 (1922)].

Xanthochymus Lineage

Leaves with prismatic crystals in the mesophyll (this character is unstudied in *Allanblackia*) (Vesque 1889, 1893). ***Flowers*** with nectariferous antesepalous appendages or intrastaminal rings and disks (sometimes manifested as lobe-like antesepalous appendages that alternate with staminodes) (Sweeney 2008, 2010; Mathew et al. 2009, Fig. 1). Staminate flowers lacking pistillodes (rarely present and then rudimentary) and anthers with globose to widely elliptic thecae.

The *Xanthochymus* lineage is comprised of Lineage A in Sweeney (2008) and *Allanblackia*. It contains three sections as circumscribed below.

1. *Garcinia* section *Xanthochymus* (Roxb.) Pierre, Fl. Forest. Cochinch. 1, Fasc. 5, 3 (1883). Clade 1

Figs 2, 3

Basionym. *Xanthochymus* Roxb., Pl. Coromandel 2(4): 51, t. 196 (1805).

Type. *Xanthochymus pictorius* Roxb. [≡*Garcinia xanthochymus* Hook.f. ex T. Anderson Fl. Brit. India [J. D. Hooker] 1(2): 269 (1874)].

Distinguishing sectional characters. ***Flowers*** usually five-merous (rarely four-merous). Staminate flowers with stamens united into fascicles with filaments united for at least ½ (usually considerably more) of their length. Pollen five- to seven-colporate (Jones 1980). Ovaries with five (rarely four) locules and a single ovule per locule, placentation axile. Afrotropics, Indomalaya, and tropical Australasia.

This section largely corresponds section *Xanthochymus* sensu Jones (1980); however, based on molecular data [this study and Sweeney (2008)] and morphology, we exclude *G. hollrungii* Lauterb. and *G. prainiana* King (and the closely allied *G. phuongmaiensis* V.S.Dang, H.Toyama & D.L.A.Tuan). We also include

here *G. conrauana* Engl. and *G. giadidii* De Wild. [=*G. kola* Heckel] – the only two species that Jones (1980) placed into section *Tetraphalangium* Engl., Bot. Jahrb. Syst. 40(4): 562 (1908), Type. *Garcinia conrauana* Engl.

Species. *Garcinia cambodgiensis* Vesque; *G. capuronii* Z.S.Rogers & P.W.Sweeney; *G. conrauana* Engl.; *G. densivenia* Engl.; *G. dulcis* (Roxb.) Kurz; *G. gamblei* Shameer, T.Sabu & N.Mohanan; *G. gerrardii* Harv. ex Sim; *G. kola* Heckel; *G. letestui* Pellegr.; *G. longifolia* Blume; *G. lowryi* Z.S.Rogers & P.W.Sweeney; *G. lucida* Vesque; *G. nervosa* (Miq.) Miq.; *G. petiolaris* Pierre; *G. pushpangadaniana* T.Sabu, N.Mohanan, Krishnaraj & Shareef; *G. quadrifaria* (Oliv.) Baill. ex Pierre; *G. spectabilis* Pierre; *G. spicata* (Wight & Arn.) Hook.f.; *G. subelliptica* Merr.; *G. talbotii* Raizada ex Santapau; *G. thwaitesii* Pierre; *G. verrucosa* Jum. & H.Perrier; *G. vidalii* Merr.; *G. vilersiana* Pierre; *G. volkensii* Engl.; *G. vriesiana* Pierre; *G. warburgiana* A.C.Sm.; *G. xanthochymus* Hook.f. ex T.Anderson.

2. *Garcinia* section *Rheedia* (L.) S.W.Jones ex P.W.Sweeney, comb. & stat. nov. Clade 2

urn:lsid:ipni.org:names:77338399-1

Figs 2, 3

Basionym. *Rheedia* L., Sp. Pl. 2: 1193 (1753).

Type. *Rheedia lateriflora* L. [=*Garcinia humilis* (Vahl.) C.D.Adams, Phytologia 20(5): 312 (1970); non *Garcinia lateriflora* Blume, Bijdr. Fl. Ned. Ind. 5: 214 (1825)].

Distinguishing sectional characters. ***Flowers*** usually with four petals (sepal number varies from two to five). Staminate flowers with stamens free or united into fascicles with filaments united up to ½ (rarely up to 2/3) of their length. Pollen tri-colporate with long ectoaperatures and endocolpi (Jones 1980). Ovaries with two to four locules and a single ovule per locule, placentation axile. Vesque (1893:288) noted that the leaves of species included in this section (i.e., species placed in the genus *Rheedia* and *Garcinia* subgenus *Rheediopsis* in his monograph) have sunken stomata with raised papilla-like protuberances arising from the accessory cells and partially covering the stomatal opening. Neotropics and Afrotropics.

This section includes species placed by Jones (1980) into sections *Rheedia* (L.) S.W.Jones *nom. inval.* (Art. 30.9, Turland et al. 2018); *Rheediopsis* Pierre, Fl. Forest. Cochinch. 1, Fasc. 5, 2 (1883), Type. *G. smeathmannii* (Planch. & Triana) N.Robson ex Spirl. (lectotype, designated here); and *Teracentrum* Pierre, Fl. Forest. Cochinch. 1, Fasc. 5, 1 (1883), Type. *G. livingstonei* T. Anderson. This section includes species that were formerly placed into the genus *Rheedia* L.

Species. *Garcinia albuquerquei* (M.E.Berg) Bittrich; *G. ambrensis* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. anjouanensis* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. aphanophlebia* Baker; *G. apostoloi* Mouzinho; *G. arenicola* (Jum. & H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. aristata* (Griseb.) Borhidi; *G. bakeriana* (Urb.) Borhidi; *G. barkeriana* (Urb. & Ekman) Alain; *G. benthamiana* (Planch. & Triana) Pipoly; *G. brasiliensis* Mart.; *G. calcicola* (Jum. & H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. cincta* (Urb.) Borhidi; *G. clarensis* Borhidi; *G. commersonii* (Planch. & Triana) Vesque; *G. cubensis* (Borhidi) Borhidi; *G. dalleizettei* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. decussata* C.D.Adams; *G. floribunda* Miq.;

G. fluviatilis Mouzinho & L.Marinho; *G. gabonensis* Sosef & Dauby; *G. gardneriana* (Planch. & Triana) Zappi; *G.* × *guacopary* (S.Moore) M.Nee; *G. hessii* (Britton) Alain; *G. humilis* (Vahl) C.D.Adams; *G. intermedia* (Pittier) Hammel; *G. kingaensis* Engl.; *G. leptophylla* Bittrich; *G. livingstonei* T.Anderson; *G. macrophylla* Mart.; *G. madruno* (Kunth) Hammel; *G. magnifolia* (Pittier) Hammel; *G. magnophylla* (Cuatrec.) Hammel; *G. mangorensis* (R.Vig. & Humbert) P.W.Sweeney & Z.S.Rogers; *G. martinii* (Maguire) Govaerts; *G. megistophylla* P.W.Sweeney & Z.S.Rogers; *G. moaensis* (Bisse) Borhidi; *G. obliqua* Sosef & Dauby; *G. ophiticola* (Borhidi) Borhidi; *G. ovalifolia* Oliv.; *G. pachyclada* N.Robson; *G. parviflora* Benth.; *G. pervillei* (Planch. & Triana) Vesque; *G. polyneura* (Urb.) Borhidi; *G. portoricensis* (Urb.) Alain; *G. pulvinata* (Planch. & Triana) Hammel; *G. pungens* Borhidi; *G. revoluta* (Urb.) Borhidi; *G. robsoniana* Bamps; *G. ruscifolia* (Griseb.) Borhidi; *G. semseii* Verdc.; *G. serpentini* Borhidi; *G. smeathmannii* (Planch. & Triana) Oliv.; *G. spruceana* (Engl.) Mouzinho; *G. staudtii* Engl.; *G. thouvenotii* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. tsimatimia* P.W.Sweeney & Z.S.Rogers; *G. urschii* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. verticillata* Alain.

3. *Garcinia* section *Allanblackia* (Oliv.) P.W. Sweeney, comb. & stat. nov.
urn:lsid:ipni.org:names:77338400-1

Basionym. *Allanblackia* Oliv., Gen. Pl. [Benth. & Hook.f.] 1(3): 980 (1867), J. Linn. Soc., Bot. 10: 43 (1867).

Type. *Allanblackia floribunda* Oliv., J. Linn. Soc., Bot. 10: 43 (1867) [≡*Garcinia oleosperma* P.W. Sweeney, nom. nov.; non *Garcinia floribunda* Miq., Stip. Surin. Sel. 39, non *Garcinia floribunda* Mast. ex Vesque, Monogr. Phan. [A.DC. & C.DC.] 8: 488 (1893)]

Distinguishing sectional characters. ***Flowers*** five-merous. Staminate flowers with stamens united into five phalanges, anthers subsessile, two-thecous. Pollen 4-colporate (Jones 1980). Ovaries incompletely five-locular containing multiple ovules per carpel/locule, placentation parietal. Afrotropics.

Note. There are nine currently accepted species in the genus *Allanblackia* Oliv., all native to Africa (Bamps 1969; Stevens 2007; POWO 2023). Here we create the section *Allanblackia* (Oliv.) P.W. Sweeney for these species when they are treated as *Garcinia* and below provide names for them in *Garcinia*.

Species:

***Garcinia guineensis* P.W.Sweeney, nom. nov.**
urn:lsid:ipni.org:names:77338401-1

Allanblackia parviflora A.Chev., Vég. Ut. Afr. Trop. Franç. 5: 163 (1909). Type. Côte d'Ivoire: Alépé, *Chevalier 16239*.

Note. A replacement name ("nom. nov."), *Garcinia guineensis*, is created here for *Allanblackia parviflora*, because the epithet *parviflora* was used previously in *Garcinia* for a different species. The epithet *guineensis* is chosen to reflect the distribution of this species in the Upper Guinean Forest region of West Africa.

***Garcinia kisonghi* (Vermoesen) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338402-1

Allanblackia kisonghi Vermoesen, Man. Ess. Forest. Congo: 11 (1923). Type. Democratic Republic of the Congo: Mpse, *Van Naemen in Gillet s.n.*

***Garcinia kimbiliensis* (Spirlet) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338403-1

Allanblackia kimbiliensis Spirlet, Bull. Jard. Bot. État Bruxelles 29: 357 (1959). Type. Democratic Republic of the Congo: Kimbili, *Michelson 766*.

***Garcinia marienii* (Staner) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338404-1

Allanblackia marienii Staner, Bull. Jard. Bot. État Bruxelles 13: 110 (1934). Type. Democratic Republic of the Congo: Haute Nsele, *De Groof s.n.*

***Garcinia ngouniensis* P.W.Sweeney, nom. nov.**
urn:lsid:ipni.org:names:77338405-1

Allanblackia gabonensis (Pellegr.) Bamps, Bull. Jard. Bot. Natl. Belg. 39: 356 (1969). Type. Gabon: between Moubighou and Nzoundou, *Le Testu 6001*.

Note. A replacement name, *Garcinia ngouniensis*, is created here for *Allanblackia gabonensis*, because the epithet *gabonensis* was used previously in *Garcinia* for a different species. The epithet *ngouniensis* is in reference to Gabon's Ngounié province, an area where many specimens of this species have been collected.

***Garcinia oleosperma* P.W.Sweeney, nom. nov.**
urn:lsid:ipni.org:names:77338406-1

Allanblackia floribunda Oliv., J. Linn. Soc., Bot. 10: 43 (1867). Type. Cameroon: Cameroon River, *Mann 2193*.

Note. A replacement name, *Garcinia oleosperma*, is created here for the type species (*A. floribunda*) of the genus *Allanblackia*, because the epithet *floribunda* was used previously in *Garcinia* for a different species. The epithet *oleosperma* is in reference to the seeds that have a high oil content and are an important source of vegetable oil in tropical western Africa (Crockett 2015).

***Garcinia staneriana* (Exell & Mendonça) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338407-1

Allanblackia staneriana Exell & Mendonça, J. Bot. 74(Suppl.): 20 (1936). Type. Angola: Belize, *Grossweiler 8221*.

***Garcinia stuhlmannii* (Engl.) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338408-1

Allanblackia stuhlmannii (Engl.) Engl., H.G.A.Engler & K.A.E.Prantl, Nat. Pflanzenfam., Nachtr. 1: 249 (1897). Type. Tanzania: Usambara, *Holst 2296*.

***Garcinia ulugurensis* (Engl.) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338409-1

Allanblackia ulugurensis Engl., Bot. Jahrb. Syst. 28: 435 (1900). Type. Tanzania: Sudost Uluguru, *Stuhlmann 8773*.

Garcinia Lineage

Leaves with druse crystals in the mesophyll (Vesque 1889, 1893). ***Flowers*** without nectariferous antesepalous appendages or intrastaminal rings and disks (Sweeney 2010). Staminate flowers in many sections with pistillodes (but usually absent in sections *Brindonia*, *Hebradendron*, and *Macrostigma*) and anthers of various shapes.

The *Garcinia* lineage contains eight sections as circumscribed below and corresponds to Lineage B in Sweeney (2008).

4. *Garcinia* section *Paragarcinia* (Baillon) Vesque, Monogr. Phan. [A. DC. & C. DC.] 8: 254 (1893). Clade 3
Figs 2, 3

Type. *Ochrocarpos decipiens* Baill., Adansonia 11: 370 (1876) [≡*Garcinia decipiens* (Baill.) Vesque, Monogr. Phan. [A.DC. & C.DC.] 8: 482 (1893)].

Distinguishing sectional characters. ***Flowers*** with two (usually) sepals, fused in bud. Staminate flowers with a pistillode, stamens arranged into four (up to eight) fascicles with sessile to subsessile, two-thecous anthers. Ovaries four locular, stigmas weakly lobed. ***Fruits*** with smooth walls. ***Inflorescences*** terminal or axillary with few to many flowers. Afrotropics (Madagascar and Comoros).

This section contains the *Garcinia* species that were formerly placed into the segregate genus *Ochrocarpos*. The twelve species in this section are endemic to Madagascar and Comoros (Sweeney and Rogers 2008).

Species. *Garcinia cerasifer* (H.Perrier) P.F.Stevens; *G. dauphinensis* P.W.Sweeney & Z.S.Rogers; *G. decipiens* Vesque; *G. evonymoides* (Planch. & Triana)

P.W.Sweeney & Z.S.Rogers; *G. goudotiana* (Planch. & Triana) P.W.Sweeney & Z.S.Rogers; *G. madagascariensis* (Planch. & Triana) Pierre; *G. multifida* (H. Perrier) P.W.Sweeney & Z.S.Rogers; *G. orthoclada* Baker; *G. parvula* (H. Perrier) P.W.Sweeney & Z.S.Rogers; *G. pauciflora* Baker; *G. tsaratananensis* (H. Perrier) P.W.Sweeney & Z.S.Rogers.

5. *Garcinia* section *Discostigma* (Haask.) Hook.f., Gen. Pl. [Benth. & Hook.f.] 1: 174 (1862). Clade 4
Figs 2, 3

Basionym. *Discostigma* Hassk., Flora 25(2, Beibl.): 33 (1842).

Type. *Discostigma rostratum* Hassk., Flora 25(2, Beibl.): 33 (1842) [≡*Garcinia rostrata* (Hassk.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 209 (1864)].

Distinguishing sectional characters. ***Flowers*** with four sepals and petals. Staminate flowers with a pistillode, stamens arranged into four fascicles that are distally covered with sessile to subsessile, two-thecous anthers. Ovaries bilocular (or unilocular; four-locular in *G. yunnanensis*), stigmas unlobed and smooth. ***Fruits*** with a smooth surface and capped with a conspicuous discoid stigma, sepals caducous in fruits. ***Inflorescences*** terminal or axillary with few to many flowers. Indomalaya, tropical Australasia, and Oceania.

Sweeney (2008) noted that there were two groups of species placed into section *Discotigma* by Jones (1980) that differed from typical members of the section by their androecial morphology. One group of species differs by having their stamens fused to the petals and includes *G. balansae*, *G. lanessanii* Pierre, *G. terpnophylla* Thwaites, and *G. warrenii* F.Muell. The position of *G. warrenii* in the trees presented here and in Sweeney (2008) suggests that some of these species may be better placed within section *Macrostigma* (clade 9); however, our molecular analyses find strong support for placement of *G. balansae* within *Discostigma*. The second group of species is restricted to New Guinea, the Philippines, and Taiwan and includes *G. dives* Pierre, *G. hunsteinii* Lauterb., *G. linii* C. E. Chang, *G. luzoniensis* Merrill, and *G. palawanensis* Elmer (Jones 1980). This latter group is reported to have peltate anthers, like species of section Hebradendron (sensu Jones 1980); however, Jones (1980) placed them into section *Discostigma* because they share the same stamen arrangement and pollen apertures as typical members of the section. Species representing the *G. dives* group have not yet been included in molecular phylogenetic analyses. *Garcinia anomala* was placed into Section *Garcinia* by Jones (1980), but excluded from that section by Nazre et al. (2018), due to its possession of axillary inflorescences in thyrses and stamens being united into an unlobed annular mass. Fruit characters suggest that this species belongs to Section Discostigma; however, the stamens are arranged into a ring.

In our ITS phylogeny, two species not treated by Jones (1980), *G. archboldiana* A.C. Sm. and *G. engleriana* A.C.Sm., are weakly supported as sister to section *Discostigma*; however, in the chloroplast phylogeny these two species are shown as sister to a larger clade comprised of sections *Brindonia*, *Garcinia*, *Hebradendron*, and *Macrostigma*. The staminate flowers of *G. archboldiana* and *G. engleriana* lack pistillodes and they have deeply branched fascicles with numerous subpeltate anthers (Smith 1941). We leave these species unplaced.

Future molecular and morphological work may warrant the placement of these species into their own section.

Species. *Garcinia apetala* Pierre; *G. balansae* Pierre; *G. balica* Miq.; *G. binnendijkii* Pierre; *G. boerlagii* Pierre; *G. brevirostris* Scheff.; *G. cadelliana* King; *G. calophylla* Pierre; *G. calophyllifolia* Ridl.; *G. caudiculata* Ridl.; *G. cordata* Merr.; *G. cuneifolia* Pierre; *G. cuspidata* King; *G. diversifolia* King; *G. dives* Pierre; *G. dryobalanoides* Pierre; *G. enthaematoeides* Lauterb.; *G. gitingensis* Elmer; *G. grandifolia* (Choisy) Pierre; *G. hasskarlii* Pierre; *G. havilandii* Stapf; *G. holttumii* Ridl.; *G. hunsteinii* Lauterb.; *G. jensenii* W.E.Cooper; *G. keenania* Pierre; *G. kwangsiensis* Merr. ex F.N.Wei; *G. lanceola* Ridl.; *G. lancilimba* C.Y.Wu ex Y.H.Li; *G. lanessanii* Pierre; *G. linearis* Pierre; *G. linii* C.E. Chang; *G. luzoniensis* Merr.; *G. memecyloides* Ridl.; *G. merguensis* Wight; *G. microphylla* Merr.; *G. minimiflora* Ridl.; *G. minutiflora* Ridl.; *G. monantha* Ridl.; *G. multiflora* Champ. ex Benth.; *G. murtonii* Whitmore; *G. myrtifolia* A.C.Sm.; *G. novoguineensis* Vesque; *G. picrorhiza* Miq.; *G. rostrata* (Hassk.) Miq.; *G. salakensis* Pierre; *G. sampitana* Diels; *G. santisukiana* Ngerns. & Suddee; *G. sarawhensis* Pierre; *G. scaphopetala* B.L.Burtt; *G. tauensis* Lauterb.; *G. terpnophylla* Thwaites; *G. tetralata* C.Y.Wu ex Y.H.Li; *G. travancorica* Bedd.; *G. treubii* Pierre; *G. umbonata* Lauterb.; *G. versteegii* Lauterb.; *G. vitiensis* (A. Gray) Seem.; *G. wollastonii* Ridl.; *G. zichii* W.E.Cooper.

6. *Garcinia* section *Brindonia* (Thouars) Choisy, Mém. Soc. Hist. Nat. Paris 1: 230 (1823). Clade 5

Figs 2, 3

Basionym. *Brindonia* Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 339 (1806).

Type. *Brindonia oxycarpa* Thouars, Hist. Veg. Isles Austr. Afr. Ed. 2 t. 27 (1805) [≡*Garcinia oxycarpa* (Thouars) P.W.Sweeney, comb. nov.; *Garcinia indica* (Thours) Choisy Mém. syn. nov.]. The copy of *Histoire des végétaux recueillis dans les isles australes d'Afrique* ed. 2 at Kew bears the date 1805 (Baker 1894) and contains six plates (25–30) that do not have accompanying text in the main body of the publication (see also Hiern 1900). Plate 27 is labeled "*Brindonia oxycarpa*" and it depicts two flowering branches, fruit, and dissected flowers (pers. obs). This suffices as an illustration with analysis and thus *Brindonia oxycarpa* is validly published as per Articles 38.1, 38.7, and 38.8 of the ICN (Turland et al. 2018). Some (e.g. Hiern 1900) have considered *B. oxycarpa* a synonym of *Garcinia indica* (Thours) Choisy Mém. Soc. Hist. Nat. Paris 1: 230 (1823) [≡*Brindonia indica* Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 340 (1806)]; however, if these two taxa are considered synonymous, the epithet *oxcycarpa* would have priority.

Distinguishing sectional characters. ***Flowers*** with four sepals and petals. Staminate flowers without a pistillode (usually), stamens united into a single central bundle (or ring when pistillode present), anthers four-thecous (but in some species two-thecous). Ovaries multilocular, stigmas divided into distinct rays and usually papillate. ***Fruits*** in many species with furrows or grooves along the septal radii. ***Inflorescence***s terminal or axillary with one to many flowers. Afrotropics (Madagascar), Indomalaya, tropical Australasia, and Oceania.

Three species treated as section *Garcinia* by Jones (1980) (i.e., *G. costata* Hemsl. ex King, *G. maingayi* Hook.f., and *G. trianii* Pierre) form a clade sister to

clade 5, the latter largely corresponding to section *Brindona* sensu Jones (1980). While they share some features (e.g. tendency to have furrowed/grooved (very shallow in *G. maingayi* and *G. trianii*), multilocular fruits) with *Brindonia* sensu Jones (1980), they have other features (i.e., pistillodes, stamens arranged into a ring, and two-thecous anthers) that are not typical of the section. While it would be tempting to recognize a separate section for these species, pistillodes and stamens arranged into a ring are also shared by *G. atroviridis* Griff. ex T.Anderson and *G. pedunculata* Roxb. ex Buch.-Ham., two species that were included in section *Brindonia* by Jones (1980). It is noteworthy that *G. atroviridis* is the first branching lineage within clade 5, which together with the *G. costata*/*G. maingayi*/*G. trianii* clade form a basal grade within section *Brindonia* (as circumscribed here).

Garcinia usually has an indehiscent drupe or berry (Stevens 2007). The genus *Clusianthemum* Vieill. was established by Vieillard for a new Caledonian species having a capsular fruit (*C. pedicellatum* Vieill.). Later, another capsular genus, *Septogarcinia* was established by Kostermans (1962) for *S. sumbawaensis* Kosterm., from Sumbawa (Indonesia), obviously not knowing about Vieillard's *Clusianthemum*. Notably, several species of NC *Garcinia*, viz. *G. virgata* Vieill. ex Guillaumin, *G. neglecta* Vieill. and *G. comptonii* Baker f. have capsular fruits (Fig. 1). Jones (1980) did not mention *Clusianthemum* in her treatment but included *Septogarcinia* in *Garcinia* sect. *Brindonia*. Jones (1980) does not cite any NC capsular species. The newly described *G. urceolata* is also suspected of having dehiscent fruits (Munzinger et al. 2021). All these species are morphologically similar and could result from *in situ* (within NC) diversification, and all sampled species with dehiscent fruit are found in a strongly supported subclade within clade 5. We do not have sequence material of *G. septogarcinia* I.M. Turner & L.V.S. Jenn. to determine whether that character is an autapomorphy of a dehiscent fruit clade, or if it evolved at least twice, in New Caledonia and Sumbawa. Staminate floral morphology supports placement of *G. septogarcinia* I.M. Turner & L.V.S. Jenn. into section *Brindona* (Medellín-Zabala and Marinho 2015).

Species. *Garcinia adinantha* A.C.Sm. & S.P.Darwin; *G. amabilis* Kaneh. & Hatus.; *G. amboinensis* Spreng.; *G. angustifolia* A.C. Sm.; *G. assamica* J.Sarma, Shameer & N.Mohanan; *G. assugu* Lauterb.; *G. asterandra* Jum. & H.Perrier; *G. atroviridis* Griff. ex T.Anderson; *G. balimensis* A.C. Sm.; *G. bancana* Miq.; *G. beccarii* Pierre; *G. bicolorata* Elmer; *G. binucao* (Blanco) Choisy; *G. borneensis* Pierre; *G. chapelieri* (Planch. & Triana) H.Perrier; *G. cochinchinensis* (Lour.) Choisy; *G. comptonii* Baker f.; *G. conicarpa* Wight; *G. corallina* Vieill.; *G. costata* Hemsl. ex King; *G. cowa* Roxb. ex DC.; *G. crassiflora* Jum. & H.Perrier; *G. dallmannensis* Kaneh. & Hatus.; *G. delpyana* Pierre; *G. dhanikhariensis* S.K.Srivast.; *G. dioica* Blume; *G. emarginata* Lauterb.; *G. erythrosepala* Y.H.Li; *G. esculenta* Y.H.Li; *G. fruticosa* Lauterb.; *G. fusca* Pierre; *G. griffithii* T.Anderson; *G. gummi-gutta* (L.) N.Robson; *G. horsfieldiana* Pierre; *G. hygrophila* Lauterb.; *G. indica* (Thouars) Choisy; *G. klinkii* Lauterb.; *G. korthalsii* Pierre; *G. lanceifolia* Roxb.; *G. lauterbachiana* A.C.Sm.; *G. ledermannii* Lauterb.; *G. leggeae* W.E.Cooper; *G. loheri* Merr.; *G. macgregorii* Merr.; *G. macrantha* A.C.Sm.; *G. maingayi* Hook. f.; *G. maluensis* Lauterb.; *G. mestonii* F.M.Bailey; *G. microstigma* Kurz; *G. minahassensis* Pierre; *G. miquelii* Pierre; *G. myristicifolia* Pierre; *G. nigrolineata* Planch. ex T.Anderson; *G. oblongifolia* Champ. ex Benth.; *G. oligophlebia* Merr.; *G. oliveri* Pierre; *G. oreophila* Lauterb.; *G. oxycarpa* (Thours) P.W.Sweeney; *G. pachyantha* A.C.Sm.; *G. pachypetala* Lauterb.; *G. pallida* Lauterb.; *G. parvifolia* (Miq.) Miq.; *G. pedunculata* Roxb.

ex Buch.-Ham.; *G. ponapensis* Lauterb.; *G. quaesita* Pierre; *G. ramosii* Merr.; *G. riparia* A.C.Sm.; *G. rubra* Merr.; *G. rubriflora* Boerl.; *G. sabangensis* Lauterb.; *G. samarensis* Merr.; *G. schomburgkiana* Pierre; *G. segmentata* Kosterm.; *G. septogarcinia* I.M.Turner & L.V.S.Jenn.; *G. siripatanadilokii* Ngerns., Meeprom, Boonth., Chamch. & Sinbumr.; *G. solomonensis* A.C.Sm.; *G. sopsopia* (Buch.-Ham.) Mabb.; *G. stigmacantha* Pierre; *G. succifolia* Kurz; *G. sulphurea* Elmer; *G. tetrandra* Pierre; *G. teysmanniana* Scheff.; *G. trianii* Pierre; *G. urceolata* Munzinger, Bruy & M.Pignal; *G. valetoniana* Lauterb.; *G. vidua* Ridl.; *G. virgata* Vieill. ex Guillaumin; *G. viridiflora* Ridl.; *G. wallichii* Choisy; *G. xishuanbannaensis* Y.H.Li; *G. zeylanica* Roxb.

7. *Garcinia* L. section *Garcinia*. Clade 6

Figs 2, 3

Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Distinguishing sectional characters. ***Flowers*** with four sepals and four petals. Staminate flowers often with a pistillode, stamens united into a single four-lobed or four-angled bundle, anthers two-thecous. Ovaries multilocular and stigmas with or without lobes and smooth or corrugated. ***Fruits*** with a smooth surface. ***Inflorescences*** terminal and comprised of simple cymes (Nazre et al. 2018). Indomalaya and tropical Australasia.

This section was recently monographed by Nazre et al. (2018) who recognized 13 species in the section and noted that species in the section share terminal inflorescences of simple cymes, stamens united into a single four-lobed or four-angled bundle, and fruits with a smooth surface. Based on morphological and molecular data he excluded several species that were included in this section by Jones (1980); our molecular results fully support his decisions (see discussion under clade 5).

Species. *Garcinia acuticosta* Nazre; *G. celebica* L.; *G. diospyrifolia* Pierre; *G. discoidea* Nazre; *G. exigua* Nazre; *G. harmandii* Pierre; *G. mangostana* L.; *G. mangostifera* Kaneh. & Hatus.; *G. nitida* Pierre; *G. ochracea* Nazre; *G. penangiana* Pierre; *G. rigida* Miq.; *G. sangudsangud* Nazre; *G. sibeswarii* Shameer, J.Sarma, N.Mohanan & A.Begum; *G. venulosa* (Blanco) Choisy.

8. *Garcinia* section *Hebradendron* Planch. & Triana, Ann. Sci. Nat., Bot. sér. 4, 14: 349 (1860). Clade 7

Figs 2, 3

Basionym. *Hebradendron* Graham, Companion Bot. Mag. 2: 199 (1837), *nom. illeg. superfl.* The genus name *Hebradendron* is illegitimate (superfluous as per Article 52.1, Turland et al. 2018) because Graham (1837) included within it *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. ix. 1787-88 (1789) 173 [≡*Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)], the type of *Stalagmitis* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789). Later, Planchon and Triana (1860) published *Garcinia* section *Hebradendron* Planch. & Triana, Ann. Sci. Nat., Bot. sér. 4, 14: 349 (1860), which according to Article 58.1 (Turland et al. 2018) can be considered a replacement name.

Type. *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789) [≡*Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856); ≡*Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)]. See Shameer and Mohanan (2020) for a discussion about the priority of *G. cambogioides* (Murray) Headland over *G. morella* (Gaertn.) Desr.

Distinguishing sectional characters. ***Flowers*** sessile to subsessile and with four sepals and four petals. Staminate flowers without a pistillode, stamens united into a single central bundle, anthers unilocular and peltate with circumscissile dehiscence or with multiple chambers that dehisce via pores. Ovaries multilocular, stigmas lobed and variously ornamented, often papillate. ***Fruits*** with smooth surface, pedicels thick in fruit. ***Inflorescences*** axillary with one to a few flowers. Indomalaya and tropical Australasia.

Species. *Garcinia acuminata* Planch. & Triana; *G. blumei* Pierre; *G. bonii* Pit.; *G. burkillii* Whitmore; *G. calycina* Kurz; G. *cambogioides* (Murray) Headland; *G. cantleyana* Whitmore; *G. choisyiana* (Choisy) Wall. ex Planch. & Triana; *G. daedalanthera* Pierre; *G. desrousseauxii* Pierre; *G. dumosa* King; *G. fuscopetiolata* Lauterb.; *G. garciae* Elmer; *G. gaudichaudii* Planch. & Triana; *G. gjellerupii* Lauterb.; *G. grahamii* Pierre; *G. hanburyi* Hook.f.; *G. hendersoniana* Whitmore; *G. heterandra* Wall. ex Planch. & Triana; *G. hopii* H.Toyama & V.S.Dang; *G. idenburgensis* A.C.Sm.; *G. imberti* Bourd.; *G. jaweri* Lauterb.; *G. lateriflora* Blume; *G. microcarpa* Pierre; *G. microtropidiiformis* Kaneh. & Hatus.; *G. mindanaensis* Merr.; *G. murdochii* Ridl.; *G. oligantha* Merr.; *G. poilanei* Gagnep.; *G. pullei* Lauterb.; *G. rheedei* Pierre; *G. schlechteri* Lauterb.; *G. scortechinii* King; *G. subtilinervis* F.Muell.; *G. timorensis* Zipp. ex Span.; *G. uniflora* King; *G. urophylla* Scort. ex King; *G. wightii* T.Anderson.

9. *Garcinia* section *Tagmanthera* Pierre, Fl. Forest. Cochinch. Vol. 1, Fasc. 6, 17 (1883). Clade 8

Figs 2, 3

Type. *Garcinia punctata* Oliv., Fl. Trop. Afr. 1: 167 (1868).

Distinguishing sectional characters. ***Staminate flowers*** with a pistillode, stamens arranged into four (rarely two) strap-shaped fascicles each with a single row of sessile, recurved, and sometimes multilocellate anthers at the end. Ovaries four locular, stigmas weakly lobed. ***Fruits*** with smooth surface. ***Inflorescences*** terminal or axillary with one to a few flowers. Afrotropics.

Species. *Garcinia acutifolia* N.Robson; *G. afzelii* Engl.; *G. bifasciculata* N.Robson; *G. buchananii* Baker; *G. buchneri* Engl.; *G. elliotii* Engl.; *G. epunctata* Stapf; *G. huillensis* Welw. ex Oliv.; *G. lujae* de Wild.; *G. mannii* Oliv.; *G. preussii* Engl.; *G. punctata* Oliv.; *G. tanzaniensis* Verdc.

10. *Garcinia* section *Macrostigma* Pierre, Fl. Forest. Cochinch. Vol. 1, Fasc. 6, 36 (1883). Clade 9

Figs 2, 3

Type. *Garcinia latissima* Miq., Ann. Mus. Bot. Lugduno-Batavi 1: 209 (1864).

Distinguishing sectional characters. ***Staminate flowers*** lacking pistillode (usually, but rudimentary or well-developed pistillode present in some species), stamens united into central column (sometimes lobed with lobes equaling number of petals) or into completely separate antepetalous fascicles, androecium often adnate to the petals to varying degrees, anthers two-thecous. Ovaries four (three) to eight locular, stigmas unlobed and smooth or divided and papillose. ***Fruits*** with smooth walls or faintly to deeply furrowed/grooved. ***Inflorescences*** axillary or terminal with one to many flowers. Indomalaya, tropical Australasia, and Oceania.

This section includes chiefly species that were included in Jones' (1980) sections *Macrostigma*, *Mungotia*, and *Tripetalum*. This is perhaps the most heterogenous of the sections recognized here and it is difficult to point to a single character shared by all of the species in the section. Many species, especially those that were placed into sections *Macrostigma* and *Tripetalum*, often have stamen bundles adnate to the petals. It has been suggested that highly branched, anastomosing exudate-containing canals on the adaxial leaf surface may be a synapomorphy for this clade (Sweeney 2008); however, this has not been comprehensively studied across the genus and may not be a reliable character for determining sectional placement (see Cooper 2013). Many species possess leaves with elliptic, elliptic-obovate, or obovate leaves with thin, closely spaced (ca. <5 mm) secondary veins. Other possible features uniting species in the group include the presence of an exotegmen and non-garcinioid type seed germination (see Brandza 1908; Stevens 2007). Further study is needed to confirm the distribution/presence of these characters.

In the phylogeny, this clade includes three species that have been variously placed into other sections by other authors (Lauterbach 1922; Jones 1980): *G. hollrungii*, *G. prainiana*, and *G. warrenii*. In addition to molecular data, these species have morphology that supports their placement into section *Macrostigma*.

Species. *Garcinia amplexicaulis* Vieill. ex Pierre; *G. branderhorstii* Lauterb.; *G. brassii* C.T.White; *G. carolinensis* (Lauterb.) Kosterm.; *G. crassifolia* Seeth.; *G. crassinervis* (Warb.) Kosterm.; *G. cymosa* (K.Schum.) I.M.Turner & P.F.Stevens; *G. densiflora* Pierre; *G. gibbsiae* S.Moore; *G. hollrungii* Lauterb.; *G. latissima* Miq.; *G. moselleyana* Pierre; *G. multibracteolata* Merr.; *G. mungotia* Planch. ex Pierre; *G. nuntasaenii* Ngerns. & Suddee; *G. pachycarpa* (A.C.Sm.) Kosterm.; *G. pancheri* Pierre; *G. pedicellata* (G.Forst.) Seem.; *G. phuongmaiensis* V.S.Dang, H.Toyama & D.L.A.Tuan; *G. platyphylla* A.C.Sm.; *G. prainiana* King; *G. pseudoguttifera* Seem.; *G. puat* (Montrouz.) Guillaumin; *G. quadrilocularis* Seeth.; *G. russellii* W.E.Cooper; *G. sessilis* (G. Forst.) Seem.; *G. smithii* Kosterm.; *G. vieillardii* Pierre; *G. warrenii* F.Muell.

11. *Garcinia* section *Dicrananthera* Pierre, Fl. Forest. Cochinch. 1, Fasc. 6, 8 (1883).

Type. *Garcinia thorelii* Pierre, Fl. Forest. Cochinch. t. 62.

Distinguishing sectional characters. ***Leaves*** with prominent stipuliform structures. Staminate flowers with a pistillode, stamens united into an annular mass encircling and attached to the pistillode, anthers two-thecous. Ovaries one to two locular, stigmas unlobed and smooth. ***Fruits*** with smooth walls. ***Inflorescences*** axillary or terminal with three to many flowers. Indomalaya.

Garcinia nujiangensis C.Y.Wu & Y.H.Li occupies an isolated position in the phylogeny, in a polytomy with clades 4 and 9. We resurrect Pierre's section *Dicrananthera* for a morphologically coherent group of species that was designated the "*Garcinia stipulata*" group in Sweeney et al. (2022). Jones (1980) treated this group, using Pierre's sectional name, as a subsection of *Discostigma* (*Garcinia* section *Discostigma* subsection *Dicrananthera* (Pierre) S.W.Jones *nom. inval.* Art. 30.9, Turland et al. 2018). Species in this group collectively range from eastern India and Bhutan, east to southwest China, and south to Myanmar and Laos. In addition to *G. nujiangensis*, the section contains *G. yaatapsap* K. Armstr. & P.W. Sweeney, *G. paucinervis* Chun & F.C.How (1956: 12), *G. stipulata* T.Anderson, and *G. thorelii* Pierre (1882: t. [plate] 62). These species all share prominent stipuliform structures (rare in Clusiaceae, Stevens 2007), leaves with prominent, widely spaced, curved secondary veins and percurrent tertiaries, staminate flowers with numerous stamens united into an annular mass encircling and attached to the pistillode (in *G. paucinervis* and *G. nujiangensis* the stamens are described as being in four bundles (Chun and How 1956; Li 1981)), and ellipsoid fruits with a discoid stigma and one to two seeds. Future molecular phylogenetic analyses will confirm if species of the 'stipulata' group are monophyletic and whether they will remain a distinct clade separate from clade 4/section *Discostigma*.

Species. *Garcinia nujiangensis* C.Y.Wu & Y.H.Li; *G. paucinervis* Chun & F.C.How; *G. stipulata* T.Anderson; *G. thorelii* Pierre; *G. yaatapsap* K.Armstr. & P.W.Sweeney.

Unplaced species

Garcinia anomala Planch. & Triana; *G. archboldiana* A.C.Sm.; *G. blancoi* Pierre; *G. bracteata* C.Y.Wu ex Y.H.Li; *G. busuangaensis* Merr.; *G. caloneura* Boerl.; *G. ceramica* Boerl.; *G. clusiifolia* Ridl.; *G. engleriana* A.C.Sm.; *G. erythrosperma* Lauterb.; *G. fagraeoides* A.Chev.; *G. graminea* Kosterm.; *G. ituman* Merr.; *G. jelinckii* Kurz; *G. klossii* Ridl.; *G. linearifolia* Elmer; *G. longipedicellata* Kosterm.; *G. lucens* Pierre; *G. mammeoides* Kosterm.; *G. matsudae* Kaneh.; *G. montana* Ridl.; *G. moszkowskii* Lauterb.; *G. moulmeinensis* Pierre ex Vesque; *G. nubigena* Lauterb.; *G. pacifica* Merr.; *G. pallide-sanguinea* Lauterb.; *G. plena* Craib; *G. propinqua* Craib; *G. qinzhouensis* Y.X.Liang & Z.M.Wu; *G. ramulosa* Lauterb.; *G. rhizophoroides* Elmer; *G. rumiyo* Kaneh.; *G. rupestris* Lauterb.; *G. schraderi* Lauterb.; *G. squamata* Lauterb.; *G. subfalcata* Y.H.Li & F.N.Wei; *G. torensis* Lauterb.; *G. tuberculata* Lauterb.; *G. whitfordii* Merr.; *G. wichmannii* Lauterb.

Taxonomy of the NC *Garcinia* species

The phylogenetic framework estimated in this study does not support the distinction between *G.* sp. "JT814" and *G. balansae* within NC, nor recover four species with multiple accessions as monophyletic (viz. *G. pedicellata*, *G. puat*, *G. comptonii*, *G. neglecta*), but confirms the distinction between NC species and both *G. vitiensis* and *G. adinantha* found in Fiji. Therefore, all NC species should still be considered as endemics. Also, *G. balansae* (belonging to clade 4/section *Discostigma*) appears more closely related to species from Fiji (*G. myrtifolia*, *G. vitiensis*), Australia (*G. jensenii*) and southeast Asia (*G. brevirostris*, *G. merguensis*, *G. rostrata*, *G. lancilimba*, *G. tetralata*) than to any other NC species.

The four species with capsular fruits (*G. comptonii*, *G. neglecta*, *G. urceolata* and *G. virgata*; retrieved in clade 5/section *Brindonia*) cannot be distinguished based on the present molecular data, but they form two pairs of species based on morphology and ecology. *Garcinia urceolata* and *G. virgata* have small leaves and were confused for a long time but differ by their flowers (green urceolate versus yellowish cup-like corolla), leaves and fruits. Both occur in dense humid forest on non-ultramafic substrates, but *G. urceolata* grows at higher elevation and in wetter conditions than *G. virgata*. *G. comptonii* appears restricted to maquis or forest edges on ultramafic substrates, while *G. neglecta* is mostly a forest tree on ultramafic and non-ultramafic substrates.

In the other NC clade (included in clade 9/section *Macrostigma*), *G. vieillardii* is restricted to the northeast dense humid forest on non-ultramafic soils, above 550 m a.s.l., while *G. densiflora* occurs in the same area and also on non-ultramafic substrates but at lower elevation. In addition, it is more a rupicolous species. The three other species can be found on both substrates (ultramafic and non-ultramafic). *Garcinia puat* is restricted to dense humid forest at low elevations, while *G. pedicellata* is a coastal (including small islands) to medium elevation tree, growing in drier conditions than the three previously cited species. Finally, *G. amplexicaulis* is the species with the widest ecological amplitude, growing in open maquis to closed humid forest, from low to 900 m a.s.l., throughout all the main island.

Conclusions

This study offers a way forward on a revised infrageneric classification of the species-rich genus *Garcinia*, based on both evolutionary history (as informed by molecular phylogenies) and morphology. We recognize eleven sections within *Garcinia*, list representative species and document distinctive morphological features for each. This classification provides an evolutionary-based foundation for future, much needed monographic work within the genus. Although additional phylogenetic analyses are warranted, by including more species and increasing the phylogenetic resolution, our phylogenetic results are a major contribution to the understanding of the evolutionary history of the genus and they provide a starting point for more ecological and evolutionary investigations as well as conservation planning and taxonomic work. Future revisionary efforts focused on some of the more speciose sections/clades recognized here (*Brindonia*, *Discostigma*, and *Hebradendron*) will certainly result in many species being reduced to synonymy and some new species being described. This was the case with a recent revision of Section *Garcinia* (Nazre et al. 2018). And, as more detailed taxonomic work is done, some species section reassignments are inevitable as are the erection of new sections to accommodate newly discovered clades with distinct suites of morphological characters.

One area that is particularly attractive for future research concerns the biogeographic history of the genus. A more complete knowledge of the spatio-temporal history of *Garcinia* would allow for a better understanding of the events that lead to the present geographic distribution of the genus. This would contribute to a growing body of knowledge about the biogeography of pantropically distributed clades and would provide additional data for exploring hypotheses about intercontinental disjunctions (e.g. Clayton et al. 2009; Couvreur et

al. 2011; Baker and Couvreur 2013; Ruhfel et al. 2016; Torke et al. 2022). At a smaller scale, studying the origin of the ten endemic NC *Garcinia* species would also be valuable. Species diversification probably occurred after colonization of the territory by long-distance colonization and recent studies on other plant groups showed that in addition to the closest and largest landmass that is Australia, diverse geographic origins could be revealed (e.g. Duangjai et al. 2009; Del Rio et al. 2017; Samuel et al. 2019).

Acknowledgements

We are grateful to all collectors in the field, and to Herbaria BO, BRI, CANB, MIN, MO, NOU, NY, P and SING for providing leaf material for DNA extraction. We also thank Kevin Maurin for lab work, Kanchi Gandhi for guidance on taxonomic matters, and Germinal Rouhan for help throughout this study. The Muséum national d'Histoire naturelle (MNHN) and the Institut de Recherche pour le Développement (IRD) provided access to the collections in the framework of the Récolnat National Research Infrastructure (ANR-11-INBS-0004). Some specimens were collected during the expedition "Our Planet Reviewed Papua-New-Guinea 2012–2013". We thank the Environmental Services of North and South Province of New Caledonia for providing collection permits.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was supported by the Muséum National d'Histoire Naturelle through the ATM Génomique & Collections and ATM Blanche.

Author contributions

Conceptualization: PS, JM, MG. Data curation: JM, PS, MG. Formal analysis: MG, PS. Funding acquisition: MG. Investigation: PS, MG. Writing - original draft: MG, PS, JM.

Author ORCIDs

Patrick Sweeney https://orcid.org/0000-0003-1239-189X
Jérôme Munzinger https://orcid.org/0000-0001-5300-2702

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Atkins HJ, Bramley GL, Nishii K, Möller M, Olivar JE, Kartonegoro A, Hughes M (2021) Sectional polyphyly and morphological homoplasy in Southeast Asian *Cyrtandra*

(Gesneriaceae): Consequences for the taxonomy of a mega-diverse genus. Plant Systematics and Evolution 307(6): 60. https://doi.org/10.1007/s00606-021-01784-x

Baker EG (1894) Notes on Guttiferae. Le Journal de Botanique 32: 360–364.

Baker WJ, Couvreur TL (2013) Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. Journal of Biogeography 40(2): 274–285. https://doi.org/10.1111/j.1365-2699.2012.02795.x

Bamps P (1969) Notes sur les Guttiferae d'Afrique tropicale. Bulletin du Jardin botanique National de Belgique 39: 345–372. https://doi.org/10.2307/3667572

Brandza G (1908) Recherches anatomiques sur la germination des Hypéricacées et des Guttifères. Annales des Sciences Naturelles-Botanique 9(8): 221–300.

Chun WY, How FC (1956) Species novae arborum utilium Chinae meridionalis. Acta Phytotaxonomica Sinica 5: 1–25.

Clayton JW, Soltis PS, Soltis DE (2009) Recent long-distance dispersal overshadows ancient biogeographical patterns in a pantropical angiosperm family (Simaroubaceae, Sapindales). Systematic Biology 58(4): 395–410. https://doi.org/10.1093/sysbio/syp041

Cooper WE (2013) A taxonomic revision of *Garcinia* L. (Clusiaceae) in Australia, including four new species from tropical Queensland. Austrobaileya 9(1): 1–29. https://doi.org/10.5962/p.299833

Couvreur TL, Pirie MD, Chatrou LW, Saunders RM, Su YC, Richardson JE, Erkens RH (2011) Early evolutionary history of the flowering plant family Annonaceae: Steady diversification and boreotropical geodispersal. Journal of Biogeography 38(4): 664–680. https://doi.org/10.1111/j.1365-2699.2010.02434.x

Crockett SL (2015) *Allanblackia* oil: Phytochemistry and use as a functional food. International Journal of Molecular Sciences 16(9): 22333–22349. https://doi.org/10.3390/ijms160922333

Del Rio C, Hennequin S, Rouhan G, Ebihara A, Lowry PP, Dubuisson J-Y, Gaudeul M (2017) Origins of the fern genus *Hymenophyllum* (Hymenophyllaceae) in New Caledonia: Multiple independent colonizations from surrounding territories and limited in situ diversification. Taxon 66(5): 1041–1064. https://doi.org/10.12705/665.4

Duangjai S, Samuel R, Munzinger J, Forest F, Wallnöfer B, Barfuss MHJ, Fischer G, Chase MW (2009) A multi-locus plastid phylogenetic analysis of the pantropical genus *Diospyros* (Ebenaceae), with an emphasis on the radiation and biogeographic origins of the New Caledonian endemic species. Molecular Phylogenetics and Evolution 52(3): 602–620. https://doi.org/10.1016/j.ympev.2009.04.021

Edgar RC (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Engler A (1894) Guttiferae. In: Engler A, Prantl K (Eds) Die natürlichen Pflanzenfamilien. Vol 3. Engelmann, Leipzig, 194–242.

Engler A (1925) Guttiferae. In: Engler A, Prantl K (Eds) Die natürlichen Pflanzenfamilien. Vol. 21, 2nd edn. Engelmann, Leipzig, 154–237.

Espirito Santo BLSD, Santana LF, Kato WH Junior, de Araújo FDO, Bogo D, Freitas KDC, Guimarães RDCA, Hiane PA, Pott A, Filiú WFDO, Arakaki Asato M (2020) Medicinal potential of *Garcinia* species and their compounds. Molecules (Basel, Switzerland) 25(19): 4513. https://doi.org/10.3390/molecules25194513

Graham R (1837) *Hebradendron*. Companion to the Botanical magazine 2: 199.

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium 41: 95–98.

Hemsley WB (1895) The flora of Tonga or friendly islands, with descriptions of and notes on new or remarkable plants, partly from the Solomon Islands. Journal of the Linnean Society of London, Botany 30(207): 158–217. https://doi.org/10.1111/j.1095-8339.1894.tb02394.x

Hiern WP (1900) Bibliographical Notes. XXV. Aubert Du Petit-Thouars. Le Journal de Botanique 38: 492–494.

Jones SW (1980) Morphology and major taxonomy of *Garcinia* (Guttiferae). PhD Thesis, University of Leicester. https://www.proquest.com/dissertations-theses/morphology-major-taxonomy-garcinia-guttiferae/docview/301438677/se-2

Kostermans AJGH (1962) Miscellaneous botanical notes 3. Reinwardtia 6(2): 155–187.

Lauterbach C (1922) Beitrage zur Flora von Paupasien, series IX. 80. Die Guttiferen Paupasiens. Botanische Jahrbücher für Systematik 58(1): 1–49.

Li YH (1981) Some new species of the genus *Garcinia* from South China. Acta Phytotaxonomica Sinica 19: 490–492.

Li X, Li J, Stevens P (2007) *Garcinia*. In: Wu Z, Raven PH, Hong DY (Eds) Flora of China. Vol. 13 (Clusiaceae through Araliaceae). Missouri Botanical Garden Press, St. Louis, 40–47.

Lowry PP, Munzinger JM (2015) Identification d'espèces végétales potentiellement menacées des sites de Tiébaghi et Camp des Sapins. Missouri Botanical Garden, Saint-Louis.

Maheshwari JK (1964) Taxonomic Studies on Indian Guttiferae III. The Genus *Garcinia* Linn. s.l. Bulletin of the Botanical Survey of India 6(2–4): 107–135.

Mathew MM, Munjuga MR, Ndangalasi HJ, Cordeiro NJ (2009) Aspects of the Floral and Fruit Biology of *Allanblackia stuhlmannii* (Clusiaceae), an Endemic Tanzanian Tree. Journal of East African Natural History 98(1): 79–93. https://doi.org/10.2982/028.098.0106

Medellín Zabala DM (2015) Sistemática del género *Garcinia* (Clusiaceae): revisión taxonómica para Colombia y filogenia de las especies Neotropicales. PhD Thesis, Universidad Nacional de Colombia.

Medellín-Zabala DM, Marinho LC (2015) *Garcinia sumbawaensis* comb. nova (Clusiaceae) based on *Septogarcinia sumbawaensis*. Annales Botanici Fennici 52(5–6): 381–382. https://doi.org/10.5735/085.052.0520

Mohanan N, Shameer PS, Sabu T (2023) Taxonomic revision of *Garcinia* (Clusiaceae) in India. Rheedea 33(3): 101–158. https://doi.org/10.22244/rheedea.2023.33.03.01

Moonlight PW, Ardi WH, Padilla LA, Chung KF, Fuller D, Girmansyah D, Hollands R, Jara-Muñoz A, Kiew R, Leong WC, Liu Y, Mahardika A, Marasinghe LDK, O'Connor M, Peng C-I, Pérez ÁJ, Phutthai T, Pullan M, Rajbhandary S, Reynel C, Rubite RR, Sang J, Scherberich D, Shui Y-M, Tebbitt MC, Thomas DC, Wilson HP, Zaini NH, Hughes M (2018) Dividing and conquering the fastest-growing genus: Towards a natural sectional classification of the mega-diverse genus *Begonia* (Begoniaceae). Taxon 67(2): 267–323. https://doi.org/10.12705/672.3

Morat P, Jaffré T, Tronchet F, Munzinger J, Pillon Y, Veillon J-M, Chalopin M, Birnbaum P, Rigault F, Dagostini G, Tinel J, Lowry PP II (2012) Le référentiel taxonomique Florical et les caractéristiques de la flore vasculaire indigène de la Nouvelle-Calédonie. Adansonia 34(2): 179–221. https://doi.org/10.5252/a2012n2a1

Mouzinho T, Soares MDL, Cabral FN, Marinho LC (2022) Nomenclatural and taxonomic novelties in *Garcinia* (Clusiaceae) from Amazonian forest. Phytotaxa 548(1): 91–98. https://doi.org/10.11646/phytotaxa.548.1.8

Müller K (2005) SeqState: Primer design and sequence statistics for phylogenetic DNA data sets. Applied Bioinformatics 4: 65–69. https://doi.org/10.2165/00822942-200504010-00008

Munzinger J, Bruy D, Pignal M (2021) Novitates neocaledonicae XI: A new endemic species of *Garcinia* L. (Clusiaceae), with an emended description of *G. virgata* Vieill. ex Guillaumin. Adansonia 43(6): 49–60. https://doi.org/10.5252/adansonia-2021v43a6

Munzinger J, Morat P, Jaffré T, Gâteblé G, Pillon Y, Rouhan G, Bruy D, Veillon J-M, Chalopin M (2023) [continuously updated] FLORICAL: Référentiel de la flore indigène vasculaire de Nouvelle-Calédonie. http://publish.plantnet-project.org/project/florical

Nazre M (2006) Taxonomic revision and molecular studies of *Garcinia* section *Garcinia*. PhD Thesis, University of Edinburgh and Royal Botanic Gardens of Edinburgh, UK.

Nazre M, Newman MF, Pennington RT, Middleton DJ (2018) Taxonomic revision of *Garcinia* section *Garcinia* (Clusiaceae). Phytotaxa 373(1): 1–52. https://doi.org/10.11646/phytotaxa.373.1.1

Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Sweden.

Pedraza-Chaverri J, Cárdenas-Rodríguez N, Orozco-Ibarra M, Pérez-Rojas JM (2008) Medicinal properties of mangosteen (*Garcinia mangostana*). Food and Chemical Toxicology 46(10): 3227–3239. https://doi.org/10.1016/j.fct.2008.07.024

Pierre L (1882) Flore Forestière de la Cochinchine, Vol. 1, Fascicle 4. Doin, Paris.

Pierre L (1883) Flore Forestière de la Cochinchine, Vol. 1, Fascicles 5 & 6. Doin, Paris.

Planchon JE, Triana J (1860) Mémoire sur la famille des Guttifères. Annales des Sciences Naturelles Botanique, 4e série, 14: 226–367

POWO (2023) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. http://www.plantsoftheworldonline.org/ [Retrieved 21 September 2023]

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. http://beast.bio.ed.ac.uk/Tracer

Rogers ZS, Sweeney PW, Gautier L (2011) Malagasy *Garcinia* (Clusiaceae) revisited: New combinations and lectotypifications for *Ochrocarpos goudotianus* and *O. evonymoides* and the lectotypification of *Garcinia comorensis*. Candollea 66(2): 2–4. https://doi.org/10.15553/c2011v662a23

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2011) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Ruhfel BR, Bittrich V, Bove CP, Gustafsson MHG, Philbrick CT, Rutishauser R, Xi Z, Davis CC (2011) Phylogeny of the clusioid clade (Malpighiales): Evidence from the plastid and mitochondrial genomes. American Journal of Botany 98(2): 306–325. https://doi.org/10.3732/ajb.1000354

Ruhfel BR, Bove CP, Philbrick CT, Davis CC (2016) Dispersal largely explains the Gondwanan distribution of the ancient tropical clusioid plant clade. American Journal of Botany 103(6): 1117–1128. https://doi.org/10.3732/ajb.1500537

Samuel R, Turner B, Duangjai S, Munzinger J, Paun O, Barfuss MHJ, Chase M (2019) Systematics and evolution of the Old World Ebenaceae, a review with emphasis on the large genus *Diospyros* and its radiation in New Caledonia. Botanical Journal of the Linnean Society 189(2): 99–114. https://doi.org/10.1093/botlinnean/boy081

Sebert H, Pancher JAI (1874) Notice sur les bois de la Nouvelle Calédonie, leur nature, leur exploitation et leurs propriétés mécaniques et industrielles, 3ème partie. Revue Maritime et Coloniale, 552–611.

Shameer P, Mohanan NN (2020) *Garcinia cambogioides*, the correct name for *G. morella* (Clusiaceae), its taxonomy, typification and notes on the status of *G. pictoria*. Rheedia 30(4): 463–469. https://doi.org/10.22244/rheedea.2020.30.04.06

Shaw J, Lickey EB, Beck JT, Farmer SB, Liu W, Miller J, Siripun KC, Winder CT, Schilling EE, Small RL (2005) The tortoise and the hare II: Relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. American Journal of Botany 92(1): 142–166. https://doi.org/10.3732/ajb.92.1.142

Shaw J, Lickey EB, Schilling EE, Small RL (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. American Journal of Botany 94(3): 275–288. https://doi.org/10.3732/ajb.94.3.275

Silvestro D, Michalak I (2012) raxmlGUI: A graphical front-end for RAxML. Organisms, Diversity & Evolution 12(4): 335–337. https://doi.org/10.1007/s13127-011-0056-0

Simmons MP, Ochoterena H (2000) Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49(2): 369–381. https://doi.org/10.1093/sysbio/49.2.369

Singh NP (1993) Clusiaceae. In: Sharma BD, Sanjappa M (Eds) Flora of India. Volume 3, Portulacaceae-Ixonanthaceae. Botanical Survey of India, Calcutta, 86–151.

Smith AC (1941) Studies of Papuasian plants, III. Guttiferae. Journal of the Arnold Arboretum 22(3): 343–374. https://doi.org/10.5962/p.185435

Smith AC (1981) Flora Vitiensis Nova: a new flora of Fiji, Vol. 2. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii.

Smith AC, Darwin SP (1974) Studies of Pacific Island plants, XXVIII. The Guttiferae of the Fijian region. Journal of the Arnold Arboretum 55(2): 215–263. https://doi.org/10.5962/p.185838

Sosef MSM, Dauby G (2012) Contribution to the taxonomy of *Garcinia* (Clusiaceae) in Africa, including two new species from Gabon and a key to the Lower Guinean species. PhytoKeys 62(17): 41–62. https://doi.org/10.3897/phytokeys.17.3114

Sprague TA (1934) *Ochrocarpos madagascariensis*. Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew) 1934(2): 88–90. https://doi.org/10.2307/4118227

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England) 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stevens PF (2007) Clusiaceae-Guttiferae. In: Kubitzki K (Ed.) The Families and Genera of Vascular Plants Flowering plants Eudicots: Berberidopsidales, Buxales, Crossosomatales, Fabales pp, Geraniales, Gunnerales, Myrtales pp, Proteales, Saxifragales, Vitales, Zygophyllales, Clusiaceae alliance, Passifloraceae alliance, Dilleniaceae, Huaceae, Picramniaceae, Sabiaceae. Springer-Verlag, Berlin, 48–66. https://doi.org/10.1007/978-3-540-32219-1_10

Sweeney PW (2008) Phylogeny and floral diversity in the genus *Garcinia* (Clusiaceae) and relatives. International Journal of Plant Sciences 169(9): 1288–1303. https://doi.org/10.1086/591990

Sweeney PW (2010) Floral anatomy in *Garcinia nervosa* and *G. xanthochymus* (Clusiaceae): A first step toward understanding the nature of nectaries in *Garcinia*. Bulletin of the Peabody Museum of Natural History 51(2): 157–168. https://doi.org/10.3374/014.051.0202

Sweeney PW, Rogers ZS (2008) Nomenclatural Notes on *Garcinia* (Clusiaceae) from Madagascar and The Comoros. Novon: A Journal for Botanical Nomenclature 18(4): 524–537. https://doi.org/10.3417/2006146

Sweeney PW, Nwe TY, Armstrong KE (2022) *Garcinia yaatapsap* (Clusiaceae), a new species from northern Myanmar. Phytotaxa 545(2): 121–127. https://doi.org/10.11646/phytotaxa.545.2.1

Torke BM, Cardoso D, Chang H, Li SJ, Niu M, Pennington RT, Stirton CH, Xu WB, Zartman CE, Chung KF (2022) A dated molecular phylogeny and biogeographical analysis reveals the evolutionary history of the trans-pacifically disjunct tropical tree genus *Ormosia* (Fabaceae). Molecular Phylogenetics and Evolution 166: 107329. https://doi.org/10.1016/j.ympev.2021.107329

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (Eds) (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten. https://doi.org/10.12705/Code.2018

van Welzen PC, Kulju KKM, Sierra SEC (2009) How to tackle revisions of large genera: Lessons from *Macaranga* and *Mallotus* (Euphorbiaceae). Blumea 54(1–3): 25–28. https://doi.org/10.3767/000651909X474078

Vesque J (1889) Epharmosis. Pars secunda: Genitalia foliaque Garciniearum et Calophyllearum. Vincennes, Paris.

Vesque J (1893) Guttiferae. In: de Candolle ALPP, de Candolle ACP (Eds) Monographiae Phanerogamarum Vol. 8. Masson, Paris.

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR Protocols: A Guide to Methods and Applications. Academic Press, San Diego, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Supplementary material 1

List of taxa and accessions used in this study

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: xlsx

Explanation note: The origin of DNA sequences is indicated, together with information on the herbarium voucher and distribution area of the taxon. In cases where the accepted name that was used in this study differed from the name provided in the original study that generated a sequence or voucher, the original name is provided (under "Prior determination") along with a reference for the taxonomic decision. Accessions that were newly sequenced in this study have boldface text. All accessions were included in the nuclear DNA phylogenetic analysis (except three samples, as indicated in the first column) and a subset was included in the chloroplast DNA phylogenetic analysis, as indicated in the corresponding column.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl1

Supplementary material 2

Molecular phylogeny of *Garcinia* L. based on *psbM-trnD* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl2

Supplementary material 3

Molecular phylogeny of *Garcinia* L. based on *trnQ-rps16* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl3

Supplementary material 4

Molecular phylogeny of *Garcinia* L. based on *rps16-trnK* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl4

Supplementary material 5

Molecular phylogeny of *Garcinia* L. based on a combined ITS and chloroplast DNA (*psbM-trnD, trnQ-rps16* and *rps16-trnK*) dataset and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl5